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REVISION OF THE GENUS *THYANTA* STÅL, 1862 (HETEROPTERA: PENTATOMIDAE) I. SOUTH AMERICA

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Abstract.—The South American species of the pentatomid genus *Thyanta* Stål are revised. The species of *Thyanta* are grouped into three subgenera based primarily on differences and similarities in male and female genitalia. The nominate subgenus contains nine species of which only three are known to occur in South America. The subgenus *Phacidium* Breddin is exclusively South American and contains eight species. Sixteen of the 20 species of *Argosoma,* new subgenus occur in South America.

Diagnoses are provided for the genus, subgenera, and the 12 previously described species. Fifteen new species are described: *T.* (*A.*) *boliviensis, T.* (*A.*) *curvata, T.* (*A.*) *emarginata, T.* (*A.*) *excavata, T.* (*A.*) *hamulata, T.* (*A.*) *infuscata, T.* (*A.*) *obtusa, T.* (*A.*) *sinuata, T.* (*A.*) *straminea, T.* (*A.*) *vadosa, T.* (*A.*) *xerotica, T.* (*P.*) *convexa, T.* (*P.*) *fimbriata, T.* (*P.*) *robusta, T.* (*T.*) *rubicunda.* The following new synonymy is recognized (junior synonym in parentheses): *T.* (*P.*) *acutangula* Jensen-Haarup, 1928 (=*T. mendozana* Jensen-Haarup, 1928; =*T. crinita* Ruckes, 1957); *T.* (*A.*) *brasiliensis* Jensen-Haarup, 1928 (=*T. humeralis* Ruckes, 1956); *T.* (*A.*) *patruelis* (Stål, 1859) (=*T. humilis* Bergroth, 1891; =*T. nitidula* Ruckes, 1956); and *T.* (*A.*) *testacea* (Dallas, 1851) (=*T. signoreti* Ruckes, 1956). Lectotypes are designated for *Cimex perditor* Fabricius, *Euschistus adjunctor* Walker, *E. fasciatus* Walker, *Pentatoma pilosum* Reed, *P. testacea, T. acutangula, T. aeruginosa* Berg, and *T. brasiliensis.* A key is provided for the South American species of *Thyanta.*

The genus *Thyanta* Stål belongs in section-one of the nominate tribe of the Pentatominae; that is, its included species lack a spine or tubercle at the base of the 3rd (2nd visible) abdominal segment. It is also characterized by an elongate ostiolar canal that reaches $\frac{3}{5}$ or more of the distance from the mesial margin of the ostiole to the lateral margin of the metapleuron. Rolston (1987) provided a key to this section that separates the seven genera in South America with a similar elongate ostiolar canal.

In the past, identifications in the genus *Thyanta* have been difficult to make because species characters were based on differences in size and coloration, both of which are extremely variable. To make determinations more manageable the genus has been artifically divided into two groups according to geographical area. The present paper reviews the species of *Thyanta* that occur in South America.

Much care is required when working with the key to species. In some cases it will be necessary to have specimens of the green form that are not discolored. When mention is made of black or brown markings on the body surface, this refers to true structural coloration. Teneral specimens and specimens of brown forms tend to become greasy and certain structures darken due to discoloration. Often there are no reliable characters to identify female specimens. Characters of the genitalia can usually be seen without dissecting the specimens, but accurate determinations may require some dissection.

When label data is cited in the text each letter in parentheses represents a separate label with (a) being closest to the specimen. Museum acronyms are defined in the acknowledgments. All measurements are in millimeters. Measurements in parentheses are of the holotype.

Thyanta Stål

Thyanta Stål, 1862a:58; Stål, 1867:529; Stål, 1872:34–35; Distant, 1880:65; Summers, 1898:45; Kirkaldy, 1909:94; Van Duzee, 1917:51; Blatchley, 1926:104, 112–113; Jensen-Haarup, 1928:185–186; Furth, 1974:21–22; Froeschner, 1981:71; McPherson, 1982:48, 76–77; Rolston and McDonald, 1984:74, 76.

Type species. Cimex perditor Fabricius, 1794 (by subsequent designation, Kirkaldy, 1909:XXX).

Diagnosis. Third (second visible) abdominal sternite lacking medial spine or tubercle. Each ostiolar ruga sulcate proximally, reaching at least ¾ distance from mesial margin of ostiole to lateral margin of metapleuron. Each buccula evanescent or arcuately truncate at posterior termination. Juga and tylus usually subequal in length; rostrum reaching at least to metacoxae. Femora unarmed; superior surface of each tibia usually sulcate. Width of scutellum at distal end of frena ⅖ or less basal scutellar width. Each paramere narrowly rounded to acute apically, lacking denticles, usually lacking lateral lobe, rarely with spinose lateral lobe.

Comments. The genus *Thyanta* is closely related to *Cyptocephala* Berg and *Tepa* Rolston and McDonald, from which it can be reliably separated only by differences in the male genitalia. Species of *Cyptocephala* and *Tepa* have the head of each paramere bearing a well-developed, apically rounded lateral lobe. Only two South American species of *Thyanta* have a similar lateral lobe, but in both species the apex of the lateral lobe is angulate or spinose. *Cyptocephala* further differs from *Tepa* and *Thyanta* in having a row of minute denticles between the lateral lobe and the apex of the paramere.

Jensen-Haarup (1928) described the subgenus *Parathyanta* within *Thyanta*. Rolston and McDonald (1984) placed *Parathyanta* as a junior synonym of *Cyptocephala*. At the same time they transferred four species from *Thyanta* to *Cyptocephala* and six species from *Thyanta* to *Tepa*. The species of both *Cyptocephala* and *Tepa* have been reviewed recently (Rolston 1972, 1986; Rider 1986b).

The genus *Thyanta* is divided into three subgenera: *Argosoma* new subgenus, *Phacidium* Breddin, and *Thyanta*. Sixteen of the 20 species of *Argosoma* occur in South America. The eight species of *Phacidium* are all restricted to South America. The nominate subgenus contains nine species, only three of which are known to occur in South America.

KEY TO SOUTH AMERICAN SPECIES OF *THYANTA*

1. Juga distinctly longer than tylus and leaving small subquadrate sinus in front of tylus (Fig. 49); superior surface of each tibia asulcate; segment 2 of each antenna at least 1.5 times length of segment 3 (southern South America) .... *aeruginosa* Berg
– Juga and tylus subequal in length or tylus slightly longer than juga; superior surface of each tibia sulcate; segment 2 of each antenna at most only slightly longer than segment 3 2

2(1). Scutellum with medial longitudinal band calloused, pale (Fig. 357), usually continuing onto pronotum; hemelytral membrane with vague fuscous band from distal end of scutellum to apex (Galapagos Islands) .... *similis* Van Duzee

– Scutellum uncalloused, occasionally a thin medial line present on pronotum; hemelytral membrane not marked as above 3

3(2). Inner basal angle of each hemelytral membrane fuscous (Fig. 337); each humeral angle narrowly rounded to nearly acute, but not spinose (Fig. 337) (Ecuador) .. .. *infuscata,* n. sp.

– Inner basal angle of each hemleytral membrane hyaline, although membrane may have distal brown flecks; each humeral angle variable, but if inner basal angle of hemelytral membrane somewhat brownish then each humeral angle spinose 4

4(3). Posterior termination of each buccula roundly truncate (Fig. 50); anterolateral pronotal margins slightly convex (Fig. 64) (Ecuador, Peru) .... *convexa,* n. sp.

– Posterior termination of each buccula evanescent (Fig. 214); anterolateral pronotal margins straight to concave 5

5(4). Exocorium and apex of corium stramineous, remainder of corium somewhat translucent, brown to green; anterior disk of pronotum stramineous, contrasting with green to brown posterior disk; humeral angles nearly spinose (Fig. 352) (Colombia, Ecuador) .... *straminea,* n. sp.

– Exocorium pale brown to green, concolorous with corium, except sometimes corium reddish, corium not translucent; coloration of pronotum variable, but if bicolored then humeral angles not spinose 6

6(5). Anterolateral and posterolateral abdominal angles piceous; humeral angles spinose 7

– Anterolateral abdominal angles never piceous; posterolateral abdominal angles variable; humeral angles variable 8

7(6). Each humeral angle weakly spinose, spines short, protruding beyond base of adjacent corium by the width of an eye or less (Fig. 16) (Galapagos Islands) .... *setigera* Ruckes

jacent corium by more than the width of an eye (Fig. 1) (southern U.S. to northern Argentina) .... *perditor* (Fabricius) (part)

8(6). Ventral surface of each humeral angle distinctly margined with piceous; humeral angles distinctly angulate or spinose 9

– Ventral surface of each humeral angle usually concolorous with rest of propleuron, sometimes becoming reddish or brownish, but not piceous; humeral angles variable, but if coloration blackish then humeral angles rounded 10

9(8). Humeral angles robustly spinose, directed anterolaterad (Fig. 124); in ventral and dorsal views posterolateral angles of pygophore appearing double-cone-shaped (Figs. 133, 134) (southern Brazil) .... *robusta,* n. sp. (part)

– Humeral angles angulate but not spinose, somewhat retrorse (Fig. 109); posterolateral angles of pygophore not double-cone-shaped in ventral and dorsal views (Figs. 118, 119) (Bolivia, Argentina, Brazil) .... *acutangula* Jensen-Haarup

10(8). Humeral angles distinctly spinose 11

– Humeral angles angulate, narrowly rounded, or broadly rounded 15

11(10). Anterolateral pronotal margins distinctly dentate for ¾ distance from head to humeral angles (Fig. 32); lateral margins of body often pink; postspiracular black spots usually lacking (Chile) .... *rubicunda,* n. sp.

– Anterolateral pronotal margins lacking teeth, or at most a few weak teeth near head; lateral margins of body not pink; postspiracular spots variable 12

12(11). Pronotum with transhumeral reddish band; mesial angles of pronotal cicatrices piceous; postspiracular black spots present; posterior margin of pygophore produced posterodorsad medially, with medial emargination (Figs. 9, 10) (southern U.S. to northern Argentina) .... *perditor* (Fabricius) (part)

– Pronotum lacking transhumeral reddish band, or if extensive areas of red present on pronotum these forming two longitudinally oblong spots near middle on posterior disk; mesial angles of pronotal cicatrices and postspiracular spots variable; posterior margin of pygophore not produced medially (Fig. 88), lacking medial emargination 13

13(12). Humeral angles rather robust, directed anterolaterad (Fig. 124); black spot on each posterolateral abdominal angle relatively large, larger than diameter of spiracle; in ventral and dorsal views posterolateral angles of pygophore appearing double-cone-shaped (Figs. 133, 134) (southern Brazil) .... *robusta,* n. sp. (part)

– Humeral angles smaller, directed laterad and usually only slightly anterad (Figs. 139, 154); black spot on each posterolateral abdominal angle lacking or if present smaller than diameter of spiracle; posterolateral angles of pygophore not double-cone-shaped (Figs. 148, 149, 163, 164) 14

14(13). Apex of head broadly rounded (Fig. 140); black spot on each posterolateral abdominal angle distinctly present; pygophore in lateral view sinuously convex (Fig. 150); in caudal view posterior pygophoral margin broadly U-shaped (Fig. 147) (southern and central South America) .... *acuta* Ruckes

– Apex of head narrowly rounded (Fig. 155); black spot on each posterolateral abdominal angle lacking or minute; pygophore in lateral view concave (Fig. 165); in caudal view posterior pygophoral margin broadly V-shaped (Fig. 162) (Venezuela, Bolivia, Brazil) .... *cornuta* Ruckes

15(10). Males 16

– Females 28

16(15). Posteroventral surface of pygophore arcuately sulcate; posterior margin of pygophore with dense fringe of long hairs (southern South America) .... *fimbriata,* n. sp. (part)

– Posteroventral surface of pygophore asulcate; posterior margin of pygophore with at most a few short hairs 17

17(16). Posteroventral surface of pygophore arcuately rounded, not produced into blunt chin-like protuberance (Chile, western Argentina) .... *juvenca* Stål (part)

– Posteroventral surface of pygophore produced into blunt chin-like protuberance 18

18(17). In ectal view each paramere armed with either a spinose or angulate lateral lobe (Figs. 203, 219) 19

– Each paramere unarmed laterally 20

19(18). In ectal view lateral lobe of each paramere triangular (Fig. 219); in medial view apex of each paramere curving dorsad and caudad forming a distinct hook (Fig. 217) (Colombia, Peru) .... *hamulata,* n. sp. (part)

– In ectal view lateral lobe of each paramere spinose (Fig. 203); in medial view apex of each paramere curving gently dorsad, but not forming distinct hook (Fig. 201) (southern South America) .... *acuminata* Ruckes (part)

20(19). Lateral walls of genital cup each with elongate black carina; roughened spiculate area on lateral surface of each paramere linear, elongate (Fig. 233) (Peru, Bolivia, northern Argentina) .... *boliviensis,* n. sp. (part)

– Lateral walls of genital cup each with black tubercle; roughened spiculate area on lateral surface of each paramere circular, localized 21

21(20). Occurring north of the equator 22

– Occurring south of the equator 26

22(21). Posterior margin of pygophore in caudal view broadly and sinuously V-shaped (Fig. 302) (Colombia, Venezuela) .... *sinuata,* n. sp. (part)

– Posterior margin of pygophore in caudal view broadly U-shaped 23

23(22). In medial view apex of each paramere rounded, angled dorsad nearly 60 degrees

from longitudinal axis of head of paramere (Fig. 287) (Venezuela) .... *curvata,* n. sp. (part)
– In medial view apex of each paramere variable, but if rounded then not angled dorsad beyond 45 degrees from longitudinal axis of head of paramere 24

24(23). In ectal view apex of each paramere obtusely rounded (Fig. 312) (Colombia, Venezuela) .... *obtusa,* n. sp. (part)
– In ectal view apex of each paramere narrowly rounded to spinose 25

25(24). In medial view each paramere with apex straight or bending slightly ventrad (Fig. 272), concave ectal surface oriented more mediad than dorsad (Trinidad and Tobago, Venezuela) .... *vadosa,* n. sp. (part)
– In medial view each paramere with apex curving gently dorsad (Fig. 171), concave ectal surface oriented more dorsad than mediad (Lesser Antilles, northern South America) .... *testacea* (Dallas) (part)

26(21). In medial view apex of each paramere spinose, lacking obtuse protuberance on shaft (Fig. 186) (central and southern South America) ....*patruelis* (Stål) (part)
– In medial view apex of each paramere usually rounded, presence of obtuse protuberance on shaft variable, but if apex of paramere is nearly spinose then protuberance is well-developed 27

27(26). In medial view apex of each paramere narrowly rounded, shaft with prominent obtuse protuberance (Fig. 247) (central and southern South America) .... *brasiliensis* Jensen-Haarup (part)
– In medial view apex of each paramere broadly rounded, shaft lacking obtuse protuberance (Fig. 324) (coastal desert from southern Ecuador to northern Chile) .... *xerotica,* n. sp. (part)

28(15). Posteromesial angle of each basal plate distinctly and moderately excavated 29
– Posteromesial angle of each basal plate rounded or only slightly emarginate 31

29(28). Concavity resulting from excavations in basal plates with sides distinctly divergent (Fig. 282) (Trinidad and Tobago, Venezuela) .... *vadosa,* n. sp. (part)
– Concavity resulting from excavations in basal plates with sides subparallel or slightly convergent 30

30(29). Concavity resulting from excavations in basal plates nearly as long as wide (Fig. 262); surface of basal plates distinctly rugose; distal end of sclerotized rod nearly linear, gradually becoming narrower towards apex (Fig. 263) (Peru) .... *emarginata,* n. sp. (part)
– Concavity resulting from excavations in basal plates distinctly wider than long (Fig. 267); surface of basal plates weakly rugose; distal end of sclerotized rod swollen subapically, narrowed apically (Fig. 268) (Colombia, Venezuela) .... *excavata,* n. sp. (part)

31(28). Distal end of sclerotized rod nearly linear, gradually becoming narrower towards apex 32
– Distal end of sclerotized rod swollen subapically, narrowed apically 34

32(31). Dilation of spermatheca constricted in middle, appearing doubly inflated (Fig. 228) (Colombia, Peru) .... *hamulata,* n. sp. (part)
– Dilation of spermatheca not constricted in middle, may be narrowed apically, but appearing as single inflation 33

33(32). Dilation of spermatheca with inflated portion abruptly narrowed for apical third, ending near apex of sclerotized rod (Fig. 258) (central and southern South America) .... *brasiliensis* Jensen-Haarup (part)
– Dilation of spermatheca with inflated portion not abruptly narrowed, reaching about ¾ distance from base to apex of sclerotized rod (Fig. 243) (Peru, Bolivia, northern Argentina) .... *boliviensis,* n. sp. (part)

34(31). Spermathecal duct swollen into distinct cylindrical structure below proximal flange (Fig. 93) (southern South America) .... *fimbriata,* n. sp. (part)
– Spermathecal duct may be swollen and coiled below proximal flange, but not forming distinct cylindrical structure 35
35(34). Dorsal punctation minute, dense, surface appearing matte (Chile, western Argentina) .... *juvenca* Stål (part)
– Dorsal punctation coarse, relatively sparse, surface glossy, shiny 36
36(35). Spermathecal duct with large amount of swelling and coiling below proximal flange, swelling carrot-shaped (Figs. 183, 198) 37
– Spermathecal duct with relatively small amount of swelling and coiling below proximal flange, swelling not carrot-shaped 38
37(36). Occurring in Lesser Antilles, Colombia, Venezuela, and Surinam .... *testacea* (Dallas) (part)
– Occurring in southern Peru and central Brazil south to Argentina .... *patruelis* (Stål) (part)
38(36). Occurring north of the equator 39
– Occurring south of the equator 41
39(38). Usually with two longitudinally oblong reddish transhumeral spots, one on each side of middle (Colombia, Venezuela) .... *curvata,* n. sp. (part)
– Dorsal surface lacking all reddish markings 40
40(39). Outer jugal margins subparallel for middle third of distance from eyes to apex of head (Fig. 309) (Colombia, Venezuela) .... *obtusa,* n. sp. (part)
– Outer jugal margins sinuous, not parallel (Fig. 301) (Colombia, Venezuela) .... *sinuata,* n. sp. (part)
41(38). Occurring in the coastal desert from southern Equador to northern Chile .... *xerotica,* n. sp. (part)
– Occurring in Bolivia, Brazil, Paraguay, and Argentina ..... *acuminata* Ruckes (part)

Subgenus *Thyanta* Stål

Diagnosis. Punctures minute, dense. Posterior termination of bucculae evanescent. Anterolateral pronotal margins straight to concave, sometimes marked with piceous; each humeral angle rounded to angulate, often spinose; pronotal cicatrices sometimes marked with piceous in mesial angles. Ostiolar canals acuminate apically. Superior surface of each tibia sulcate.

Posterior margins of basal plates sinuous, posteromesial angles entire (Fig. 13). Distal end of sclerotized rod cone-shaped (Fig. 14); spermathecal bulb digitiform; cylindrical structure present below proximal flange (Fig. 15).

Pygophoral opening small, subtended on posteroventral surface by a rectangular or semicircular impression; posterior margin of pygophore straight to concave in caudal view, with medially incised protuberance in middle (Fig. 9). Each paramere F-shaped, obtuse protuberance on shaft usually prominent, apex spinose, ectal surface convex (Fig. 3), roughened spiculate area on lateral surface linear (Fig. 4). Each lateral conjunctival lobe of aedeagus with single spinose diverticulum (Fig. 6); dorsomedial conjunctival lobe usually well-developed (Fig. 7); theca large, subtriangular in lateral view, with dorsolateral protuberance on each side near caudal limit (Fig. 8); medial penial lobes and penisfilum moderate in size.

Comments. Species of the subgenus *Thyanta* have the pygophoral opening subtended by a semicircular or rectangular impression, and the posterior margin is distinctly emarginate medially. Species of *Phacidium* have the posteroventral surface

of the pygophore arcuately rounded or sulcate, and the posterior margin not emarginate medially. The posteroventral surface of the pygophore in species of *Argosoma* is produced into a blunt chin-like protuberance. Also, species of *Argosoma* have the ectal surface of each paramere concave, while it is convex in both *Phacidium* and *Thyanta.*

The female genitalia are also useful in separating species of *Thyanta* and *Phacidium.* In *Thyanta* the distal end of the sclerotized rod is cone-shaped, and the spermathecal bulb is digitiform. In *Phacidium* the distal end of the sclerotized rod is swollen subapically and narrowed distally, and the spermathecal bulb is globose. The female genitalia of both *Phacidium* and *Argosoma* are very similar, but females can usually be separated by the relative density of the dorsal punctation. The dorsal punctation is relatively dense in *Phacidium,* while it is less dense and more coarse in *Argosoma.*

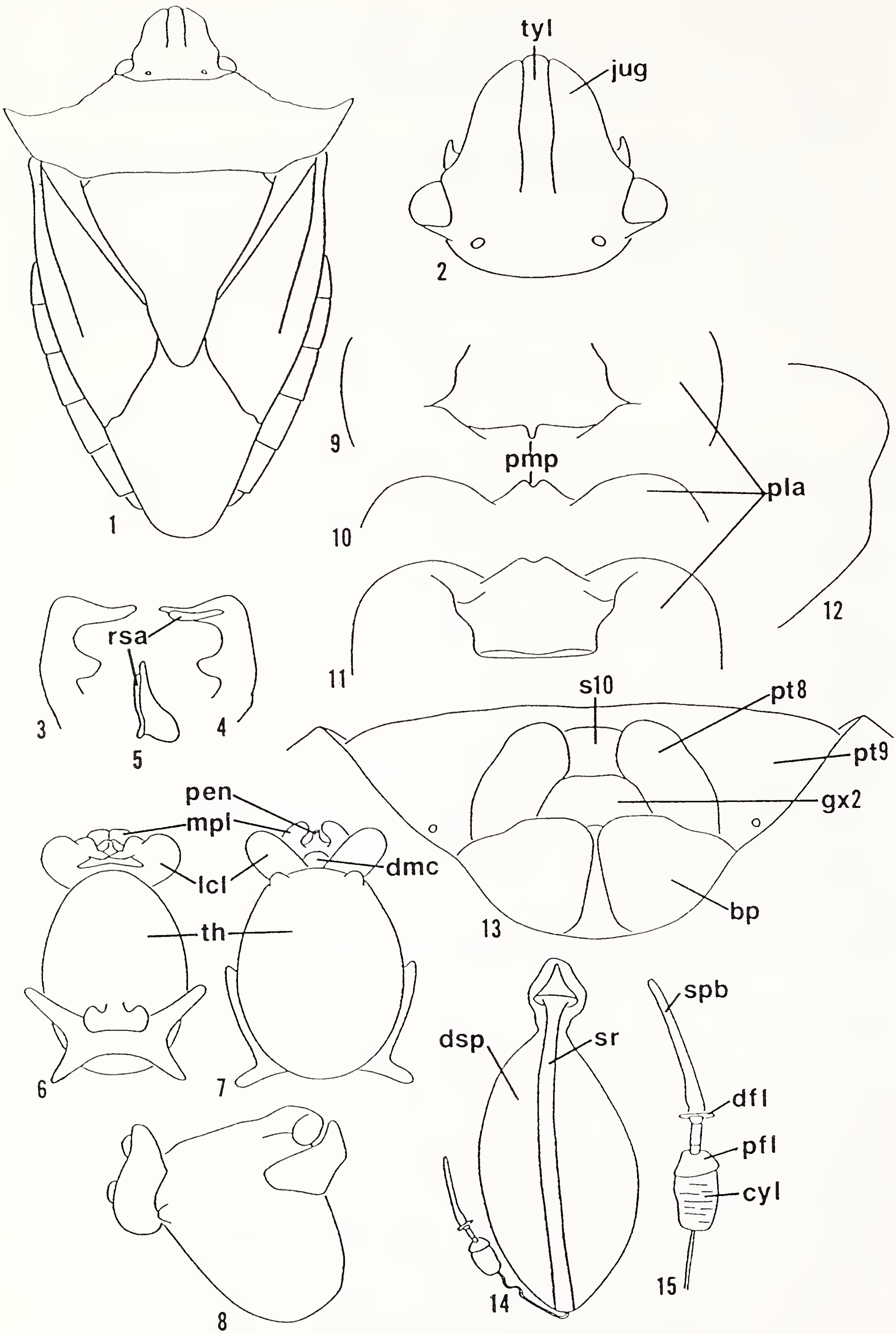
Thyanta (*Thyanta*) *perditor* (Fabricius)
Figs. 1–15, Map 1

Cimex perditor Fabricius, 1794:102; Fabricius, 1803:163.
Pentatoma fascifera Palisot de Beauvois, 1817:150, fig. 8. (syn. by Dallas, 1851)
Pentatoma collaris Westwood, 1837:40. (syn. by Dallas, 1851)
Cimex transversalis Herrich-Schäffer, 1841:66. (syn. by Dallas, 1851)
Cimex dimidiatus Herrich-Schäffer, 1841:fig. 629. (syn. by Dallas, 1851)
Pentatoma dimidiatum: Herrich-Schäffer, 1844:94.
Euschistus perditor: Dallas, 1851:206; Walker, 1867:247.
Pentatoma (*Mormidea*) *perditor:* Guérin-Méneville, 1857:367.
Thyanta perditor: Stål, 1862a:58, Stål, 1862b:104; Stål, 1868:29; Stål, 1872:34; Uhler, 1872:399 (part); Uhler, 1876:289; Uhler, 1877:404 (part); Distant, 1880:66; Berg, 1884:100; Distant, 1893:333; Lethierry and Severin, 1893:148; Uhler, 1893:705; Uhler, 1894a:230 (part); Uhler, 1894b:173; Distant, 1900b:432; Van Duzee, 1904: 52, 53 (part); Van Duzee, 1907:9; Kirkaldy, 1909:95; Banks, 1910:90; Zimmer, 1911:14 (part); Barber, 1914:523; Van Duzee, 1917:51–52; Barber, 1923:12; Blatchley, 1926:113, 114–115 (part); Barber, 1939:292–293; Torre-Bueno, 1939: 230; Ruckes, 1957a:1, 20.
Euschistus fasciatus Walker, 1867:245. (syn. by Stål, 1872)
Euschistus adjunctor Walker, 1867:249. (syn. by Stål, 1872)

Diagnosis. Transhumeral rubiginous band usually present; often tylus and vertex of head reddish.

Outer jugal margins sinuous, not parallel (Fig. 2). Each humeral angle spinose, spine directed anterolaterad and protruding beyond adjacent corium by more than half width of eye; anterolateral pronotal margins not piceous, concave in dorsal view (Fig. 1). Mesial corner of each pronotal cicatrice black. Each abdominal sternite with postspiracular black spot on each side. Both anterolateral and posterolateral angles of abdominal sternites usually piceous.

Basal plates in caudoventral view with mesial margins straight to slightly convex, separated basally; posterior margins sinuous (Fig. 13). Pygophoral opening subtended by semicircular impression; posterior margin of pygophore produced posterodorsad, in ventral and dorsal views convex medially with small medial V-shaped emargination (Figs. 10, 11); posterior margin concave in lateral view (Fig. 12).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Types. Fabricius (1794) described *Cimex perditor* from 2♀♀ and 2♂♂ without designating a holotype or paratypes. The ♂ specimen labeled (a) "C: perditor" (b) "Thyanta perditor F." is designated lectotype. The remaining ♂ and 2♀♀ are designated paralectotypes. They have the following label data: (a) "Thyanta perditor F." (♂); (a) [green paper; no writing] (b) "Thyanta perditor F." (♀); and (a) [green paper; no writing] (b) "♀" (c) "Type" (d) "Thyanta perditor F." (♀). All four specimens, which are housed in the Universetetes Zoologiske Museum (Copenhagen, Denmark), were examined.

Pentatoma fascifera Palisot de Beauvois, *P. collaris* Westwood, *Cimex transversalis* Herrich-Schäffer, and *C. dimidiatus* Herrich-Schäffer were all placed as junior synonyms of *T. perditor* by Dallas (1851). The type specimens of Herrich-Schäffer are apparently no longer in existence, but the descriptions, including the figure of *C. dimidiatus,* agree reasonably well with *T. perditor.* The type specimens for *P. fascifera* and *P. collaris* were not examined.

Pentatoma fascifera was described from Santo Domingo, Dominican Republic (Palisot de Beauvois, 1817). Although its description is rather short, it does not differ in any significant way from *T. perditor.* Also, *T. perditor* is the only species of *Thyanta* in the Dominican Republic that has distinctly spinose humeral angles.

Westwood (1837) described *P. collaris* from the island of St. Vincent in the West Indies. Its description fits *T. perditor* in all respects, and *T. perditor* is the only species of *Thyanta* with distinctly spinose humeral angles that occurs on St. Vincent.

Walker (1867) described *Euschistus fasciatus* and *E. adjunctor.* Both of these species were placed as junior synonyms of *T. perditor* by Stål (1872). In neither case did Walker designate a holotype or paratypes, and it is difficult to ascertain how many specimens he examined. *Euschistus fasciatus* was described from at least two specimens, but only one syntype was located. It is here designated lectotype and has the following label data: (a) "Type" (b) "58.135 Mex. (Oajaca)" (c) "12. EUSCHISTUS FASCIATUS." [dorsal surface], "West Indies" [ventral surface]. Only one syntype of *E. adjunctor* was located. This specimen, labeled (a) "Type" (b) "Belize" [dorsal surface], "51 117" [ventral surface] (c) "39. EUSCHISTUS ADJUNCTOR." [dorsal surface], "O varius aut ochraceus, dense p" [ventral surface], is designated lectotype. Both lectotypes were examined and are typical specimens of *T. perditor*; both are conserved at the British Museum of Natural History (London, England).

At one time *Euschistus rubiginosus* Dallas was considered a synonym of *T. perditor.*

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Figs. 1–15. *T. perditor.* 1. Habitus. 2. Head. 3–5. Right paramere. 3. Medial view. 4. Lateral view. 5. Ectal view. 6–8. Theca and related structures. 6. Ventral view. 7. Dorsal view. 8. Lateral view. 9–12. Pygophore. 9. Caudal view. 10. Ventral view. 11. Dorsal view. 12. Lateral view. 13. Genital plates, caudoventral view. 14. Spermatheca. 15. Spermathecal pump. Symbols: bp, basal plate; cyl, cylindrical structure below proximal flange; dfl, distal flange; dmc, dorsomedial conjunctibal lobe; dsp, dilation of spermatheca; gx2, second gonacoxa; jug, juga; lcl, lateral conjunctival lobe; mpl, median penial lobe; pen, penisfilum; pfl, proximal flange; pla, posterolateral angle of pygophore; pmp, posterior margin of pygophore; pt8, eighth paratergite; pt9, ninth paratergite; rsa, roughened spiculate area on lateral surface of paramere; spb, spermathecal bulb; sr, sclerotized rod; s10, tenth sternite; th, theca; tyl, tylus.

Rider (1986a), however, examined the holotype and determined that it was a species of *Euschistus* and a senior synonym of *E. incus* Rolston.

Distribution. Thyanta perditor is the most widely distributed species in the genus, occurring from the southern United States to northern Argentina (Map 1).

Specimens examined. 167 specimens collected during every month of the year; deposited in AMNH, BMNH, CAS, CELM, CU, DAR, DBT, EGER, FSCA, IIAS, LHR, QCAZ, SMEK, UCB, UNAM, UNCM, USNM. COLOMBIA: La Ceja, S. H. *Antioquia:* Bello; Medellín Valley; Sopetrán; Union. *Cundinamarca:* Silvania, 60 km SW Bogotá. *Magdalena:* San Jerónimo; Santa Marta. *Tolima:* 9 km NW Espinal. *Valle del Cauca:* Bitaco Valley, 1 km above Bitaco; Buga; Palmira; Pance, 11 km S Cali; 1 km W Yumbo. VENEZUELA: El Valle. *Lara:* Sarare. *Monagas:* 4 km S El Rosario. SURINAM: *Paramaribo:* Paramaribo. FRENCH GUIANA: *Cayenne:* Macouria. ECUADOR: Bucay; Coto Callao; Juive; Oriente Río Negro; Pallatanga. *Cotopaxi:* Pifo. *Imbabura:* Chachimbiro; Ibarra. *Morona-Santiago:* Macas, Río Upano. *Napo:* Baeza. *Pichincha:* Cugobambilla; Diluriguin; H. la Esperie; Palmeras; Pomasqui; Puembo; Pululahua; Quito; San Rafael; Tandapi; Valle de los. *Tungurahua:* Ambato Mulalillo. PERU: Valle Chanchamayo. *Amazonas:* Bagua Chica. *Ayacucho:* Huanta; Río Pampas. *Cuzco:* Macchupichu. *Huánuco:* 30 mi NE Huánuco; Pozuzo; Tingo María. *Junín:* Estancia Naranjal San Ramón. *Lima:* Barranca; Lima. BOLIVIA: Prov. Sara; Tropical. *Chuquisaca:* Monteagudo. *Cochabamba:* Prov. Chapare, Alto Palmar; Prov. Chapare, Chapare; Prov. Chapare, Christal-Mayu. *La Paz:* Coroico; Yungas de La Paz. *Santa Cruz:* Prov. Ichilo, Buena Vista. BRAZIL: Warta PR. *Ceará:* Barbalha. *Mato Grosso:* 35 mi W Araguaia; Independencia. *Minas Gerais:* Viçosa. *Pará:* Almeirim, São Raimundo. *Parañá:* 20 mi S Pato Branco. *São Paulo:* Barretos; 10 mi S Guapara. ARGENTINA: *Jujuy. Misiones. Salta:* Campo Santos de Salta.

Comments. Only three species of the nominate subgenus occur in South America, *T. perditor, T. rubicunda,* and *T. setigera. Thyanta setigera* occurs only on the Galapagos Islands and can usually be recognized by the relatively short humeral spines that protrude beyond the base of the adjacent corium by less than the width of an eye. *Thyanta rubicunda* can be identified by the strong denticulations along the anterolateral pronotal margins, and usually by the absence of black markings on the anterolateral angle of each abdominal segment. In contrast, *T. perditor* has relatively longer humeral spines that protrude beyond the base of the adjacent corium by more than the width of an eye, has the pronotal denticulations reduced and restricted to the half nearest the head, and usually has the anterolateral angle of each abdominal segment marked with black.

Thyanta (*Thyanta*) *setigera* Ruckes
Figs. 16–31

Thyanta perditor (of authors, not Fabricius): Heidemann, 1901:365; Barber, 1934: 282; Van Duzee, 1937:112.

Thyanta setigera Ruckes, 1957c:179–180, figs. 7, 8; Linsley and Usinger, 1966:133; Froeschner, 1981:71; Froeschner, 1985:43–44.

Diagnosis. Ovate. Dorsal surface green or brown, usually with at least partial transhumeral rubiginous band.

Apex of head broadly rounded; outer jugal margins sinuous, not parallel (Fig. 17). Anterolateral margins of pronotum concave in dorsal view, immaculate, with at most a few weak denticles near head; each humeral angle acute, weakly spinose, oriented laterad, spine protruding beyond base of adjacent corium by less than half width of eye (Fig. 16). Mesial angle of each pronotal cicatrice piceous. Postspiracular black spot present on both sides of each abdominal sternite; posterolateral angles and usually anterolateral angles of each abdominal sternite marked with black.

Mesial margins of basal plates in caudoventral view nearly straight, separated basally; posterior margins sinuous (Fig. 29). Pygophoral opening subtended by semicircular impression; posterior margin in caudal view distinctly convex with medial V-shaped emargination (Fig. 25), concave in lateral view (Fig. 28).

Types. Ruckes (1957c) described *T. setigera* from 24♂♂ and 27♀♀ specimens, all from the Galapagos Islands. The holotype and 27 paratypes were examined. The holotype is housed in the California Academy of Sciences (San Francisco).

Distribution. Galapagos Islands, Ecuador.

Specimens examined. 39 specimens collected between 25 February and 17 June, and on 26 November; deposited in AMNH, CAS, CU, DAR, LACM, SMEK, UCB, USNM. ECUADOR: GALAPAGOS ISLANDS: *Fernandina Island:* nr. Española Island. *Gardner Island:* nr. Española Island. *Isabela Island:* Banks Bay; Tagus Cove. *N. Seymour Island. Rábida Island. San Cristóbal Island. Santa Cruz Island:* 1.5 mi N Academy Bay; Bellavista; Conway Bay; Sullivan Bay. *Santiago Island.*

Comments. The only other species of *Thyanta* that occurs on the Galapagos Islands is *T. similis. Thyanta setigera* is easily separated from *T. similis* by the spinose humeral angles. The humeral angles are rounded in *T. similis.*

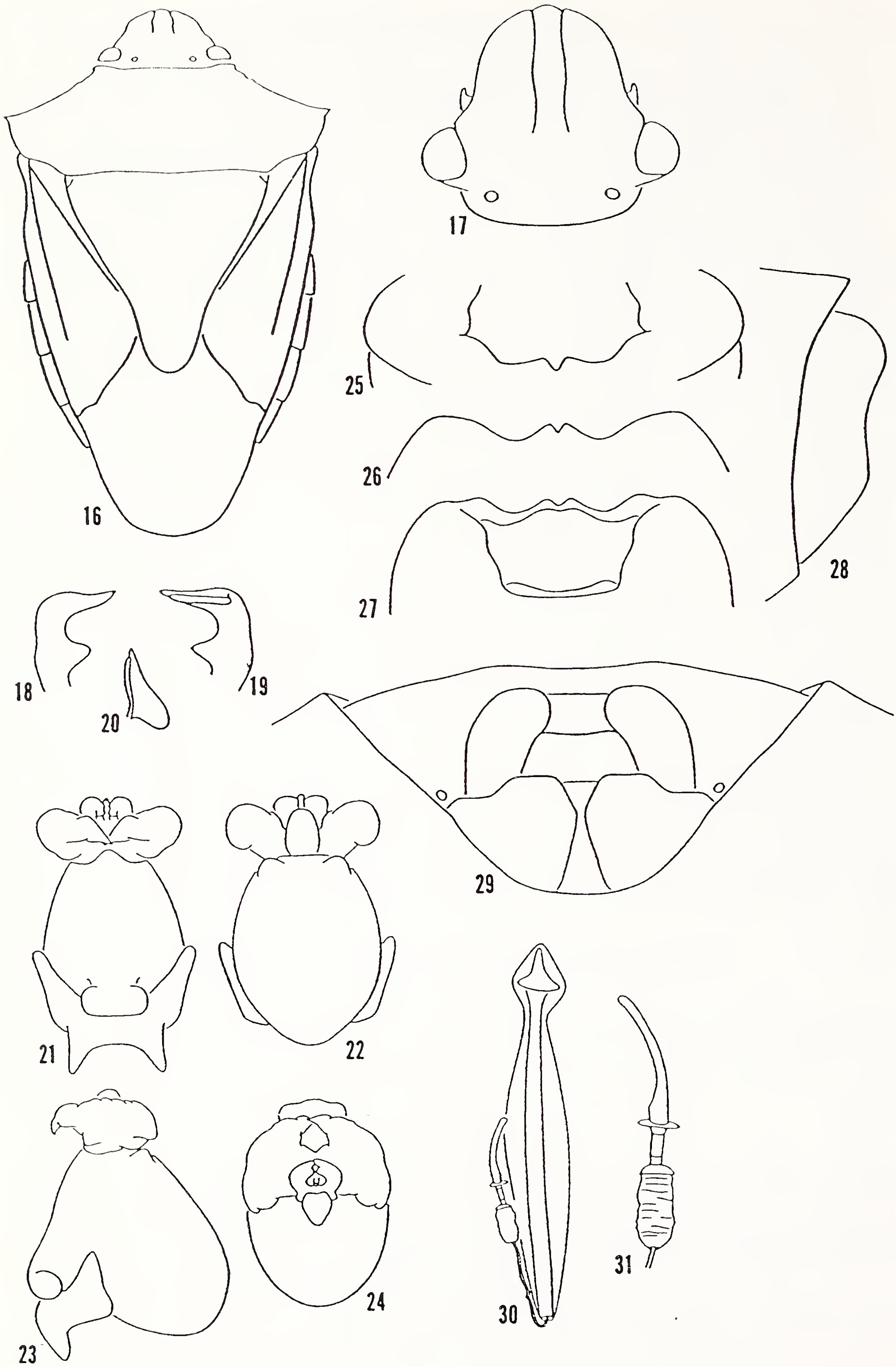
The relatively short humeral spines of *T. setigera,* protruding beyond the base of the adjacent corium by less than the width of an eye, readily distinguish this species from *T. perditor.* The only other related species occurring in South America is *T. rubicunda* which has strong denticulations along the anterolateral pronotal margins and usually lacks any black markings on the anterolateral angles of the abdominal segments. In contrast, *Thyanta setigera* has reduced pronotal denticulation and usually the anterolateral angle of each abdominal segment is marked with black.

Thyanta (Thyanta) rubicunda Rider, new species

Figs. 32–47, Map 1

Description. Elongate ovate, dorsal surface pale to medium green or brown, often with pinkish-red markings between humeri, on apex of scutellum, and along lateral margins of pronotum, coria, and connexiva; punctures usually concolorous with surface.

Apex of head broadly rounded; outer jugal margins sinuous, not parallel, only slightly concave in front of eyes (Fig. 33). Antennae pale brown to green, distal fourth of segment 3 dark brown, segments 4–5 entirely dark brown. Anterolateral pronotal margins in dorsal view concave, strongly denticulate for ⅔ distance nearest head; humeral angles spinose, oriented anterolaterad, spines relatively short (Fig. 32). Mesial angle of each pronotal cicatrice piceous. Coria densely and uniformly punctate; distal margins convex; costal angles angulate, reaching to middle of penultimate connexival segments (Fig. 32); hemelytral membranes hyaline with a few scattered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brown flecks. Connexiva narrowly exposed; posterolateral angle of each segment usually immaculate, sometimes minutely marked with black.

Ventral surface pale brown to green; punctures usually concolorous with surface. Rostrum pale brown to green, segment 4 mostly black, apex reaching between metacoxae. Femora and tibiae pale brown to green, tarsal segments and apex of each tibia darker. Postspiracular black spots lacking (except in brown form); posterolateral angles of each abdominal sternite at most minutely marked with black; anterolateral angles usually immaculate.

Mesial margins of basal plates in caudoventral view weakly concave, separated basally, almost contiguous apically; posterior margins sinuous, posteromesial angles broadly rounded (Fig. 45). Distal end of sclerotized rod cone-shaped (Fig. 46); spermathecal bulb digitiform, spermathecal duct forming distinct cylindrical structure below proximal flange (Fig. 47). Pygophoral opening subtended by semicircular impression; posterior margin nearly straight with medial V-shaped emargination in caudal view (Fig. 41); trisinuous in ventral and dorsal views (Figs. 42, 43); posterolateral angles prominent in lateral view (Fig. 44). Apex of each paramere spinose in ectal view (Fig. 36); shaft rather robust at base with small tubercle (Fig. 34); roughened, spiculate area on lateral surface linear (Fig. 35). Each lateral conjunctival lobe of aedeagus with single diverticulum (Fig. 37); dorsomedial lobe present (Fig. 38).

Measurements. Total length 8.28–10.72 (9.54); total width 5.83–7.02 (6.62); medial length of pronotum 1.62–2.13 (1.95). Medial length of scutellum 3.48–4.53 (3.86); basal width 3.20–3.75 (3.42); width at distal end of frena 1.07–1.47 (1.40). Length of head 1.72–1.90 (1.72); width 2.23–2.54 (2.30). Length of segments 1–5 of antennae 0.40–0.44 (0.44), 0.92–0.98 (0.92), 0.92–1.03 (0.92), 1.03–1.10 (1.03), and 1.07–1.14 (1.14), respectively. Length of segments 2–4 of rostrum 1.32–1.47 (1.34), 0.74–0.88 (0.77), and 0.74–0.77 (0.74), respectively.

Holotype. ♂ labeled (a) "Pocos, Antofagaste Prov. E. of Atacama Salt Lk., Chile March 1955, Luis E. Pena, Collector" (b) "*Thyanta juvenca* Stal, Lutz '57." Deposited in the American Museum of Natural History (New York).

Paratypes. 5♂♂, 13♀♀. Labeled same as holotype except (b) "J C Lutz Collection 1961" (♀ USNM); (a) "Rayado Aconc. 18-VIII-1960" (b) "L. Campos colector" (♂ IIAS); (a) "CHILE: San Pedro de Atacama, N. of Atacama Salt Lake, Antofagaster Prov. V-1–6-1964" (b) "L.E.Pena Collector" (2♀♀ AMNH); (a) "Estancia Castilla Vallenar" (b) "8- Mayo 1969.-" (c) "J.Aranda Colector" (♂ DAR; ♀ IIAS); "Chile. Vallenar 3.VII.86 En alfalfa Col. SAG" (♂ IIAS); "CHILE Pudahuel Vegetación 25.V.85 Col. R. Hevia" (♂ IIAS); (a) "Chaca (Chile?) 11-5-55 L.E. Pena" (b) "Thyanta juvenca Stal, Det. J.C. Lutz" (♀ AMNH); (a) "Chile Mamina IX.17.51" (b) "THOMAS F. HALSTEAD COLLECTION, California Academy of Sciences Accession" (♀ CAS); (a) "Rio Lluta, Arica Dept. Tarapaca Prov., Chile Nov. 11–13, 1955; 500 Mt.

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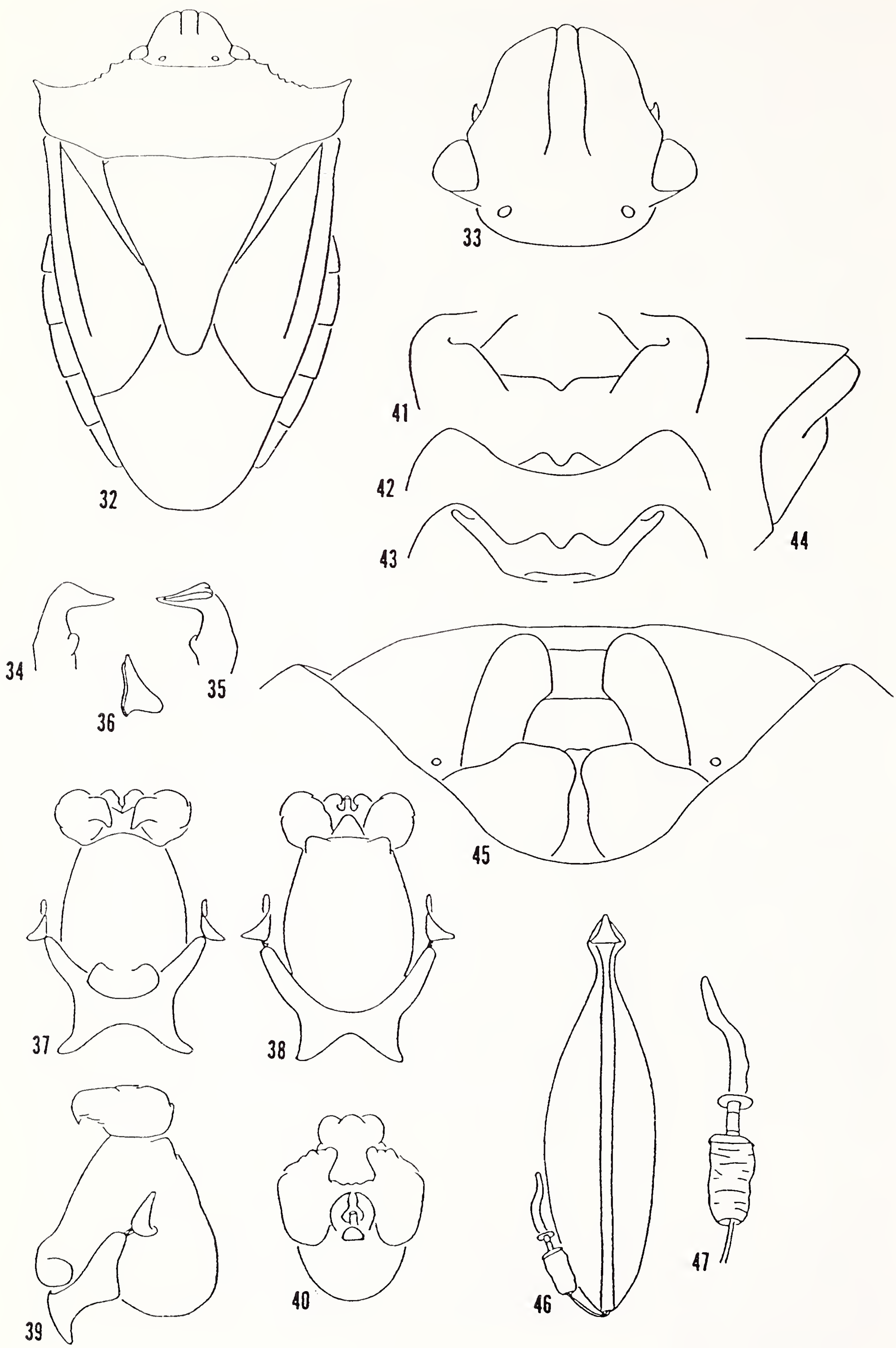
Figs. 16–31. *T. setigera.* 16. Habitus. 17. Head. 18–20. Right paramere. 18. Medial view. 19. Lateral view. 20. Ectal view. 21–24. Theca and related structures. 21. Ventral view. 22. Dorsal view. 23. Lateral view. 24. Caudal view. 25–28. Pygophore. 25. Caudal view. 26. Ventral view. 27. Dorsal view. 28. Lateral view. 29. Genital plates, caudoventral view. 30. Spermatheca. 31. Spermathecal pump.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Map. 1. *T.* (*P.*) *aeruginosa,* (■); *T.* (*P.*) *convexa,* (○); *T.* (*A.*) *curvata,* (△); *T.* (*T.*) *perditor,* (●); *T.* (*T.*) *rubicunda,* (□).

Luis E. Pena, Collector" (b) "J C Lutz Collection 1961" (c) "Thyanta juvenca Stal" (♀ USNM); (a) "LOMAS de PEÑUELAS LA SERENA -II-1953" (b) "Thyanta chilensis H.S. Det. D.B.Thomas 1978" (♀ MNHS); "LOMAS de PEÑUELAS. LA SERENA -II-1953" (♀ MNHS); (a) "Los Andes, Chile" (b) "17-V-79 Coll. G. Gordh" (♀ UCR); (a) "Peñueles 8-3-53" (b) "*Thyanta chilensis* H.S. Det. D.B. Thomas 1978" (♀ DBT); (a) "Arequipa Peru 10,28, '98" (b) "Herbert Osborn Collection" (♂ 2♀♀ OSU), except 1♀ with (c) "may be patruelis St." and 1♀ with (c) "Arequipa Oct. 30,98." (OSU).

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Figs. 32–47. *T. rubicunda.* 32. Habitus. 33. Head. 34–36. Right paramere. 34. Medial view. 35. Lateral view. 36. Ectal view. 37–40. Theca and related structures. 37. Ventral view. 38. Dorsal view. 39. Lateral view. 40. Caudal view. 41-44. Pygophore. 41. Caudal view. 42. Ventral view. 43. Dorsal view. 44. Lateral view. 45. Genital plates, caudoventral view. 46. Spermatheca. 47. Spermathecal pump.

Distribution. Peru and Chile (Map 1).

Comments. This species can be identified by the reduced amount of black markings on the abdominal venter, by the shape and orientation of each humeral spine, by the denticulation along the anterolateral pronotal margins, and usually by the pinkish coloration along the lateral margins of the body. The shape of the paramere is also unique within the nominate subgenus. The obtuse protuberance on the shaft of the paramere is reduced and nearer the base of the shaft.

Etymology. In Latin, rubicunda means pink-bordered, a character that many specimens of this species exhibit.

Subgenus *Phacidium* Breddin

Phacidium Breddin, 1912:92; Rolston and McDonald, 1984:83–84 (syn. with *Thyanta*).

Type species. Phacidium euchlorum Breddin, 1912 (by monotypy).

Diagnosis. Punctation small, relatively dense, dorsal surface appearing matte. Distal end of sclerotized rod swollen subapically, narrowed and sometimes elongate distally (Fig. 76); spermathecal bulb globose, usually with relatively large amount of coiling below proximal flange, sometimes forming cylindrical structure (Fig. 62). Posteroventral surface of pygophore arcuately rounded or with deep, broad sulcus; posterior margin entire, sinuous (Fig. 51), or sometimes broadly V-shaped (Fig. 69). Each paramere apically acute, ectal surface convex (Fig. 58), lacking dorsomedial concave surface.

Comments. The male genitalia are useful in separating species of *Phacidium* from species of the other two subgenera (see comments under subgenus *Thyanta*). The female genitalia are also useful in separating species of *Phacidium* and *Thyanta*. Females of *Argosoma* can be recognized by their relatively sparse and coarse dorsal punctation.

Thyanta (*Phacidium*) *aeruginosa* Berg
Figs. 48–63, Map 1

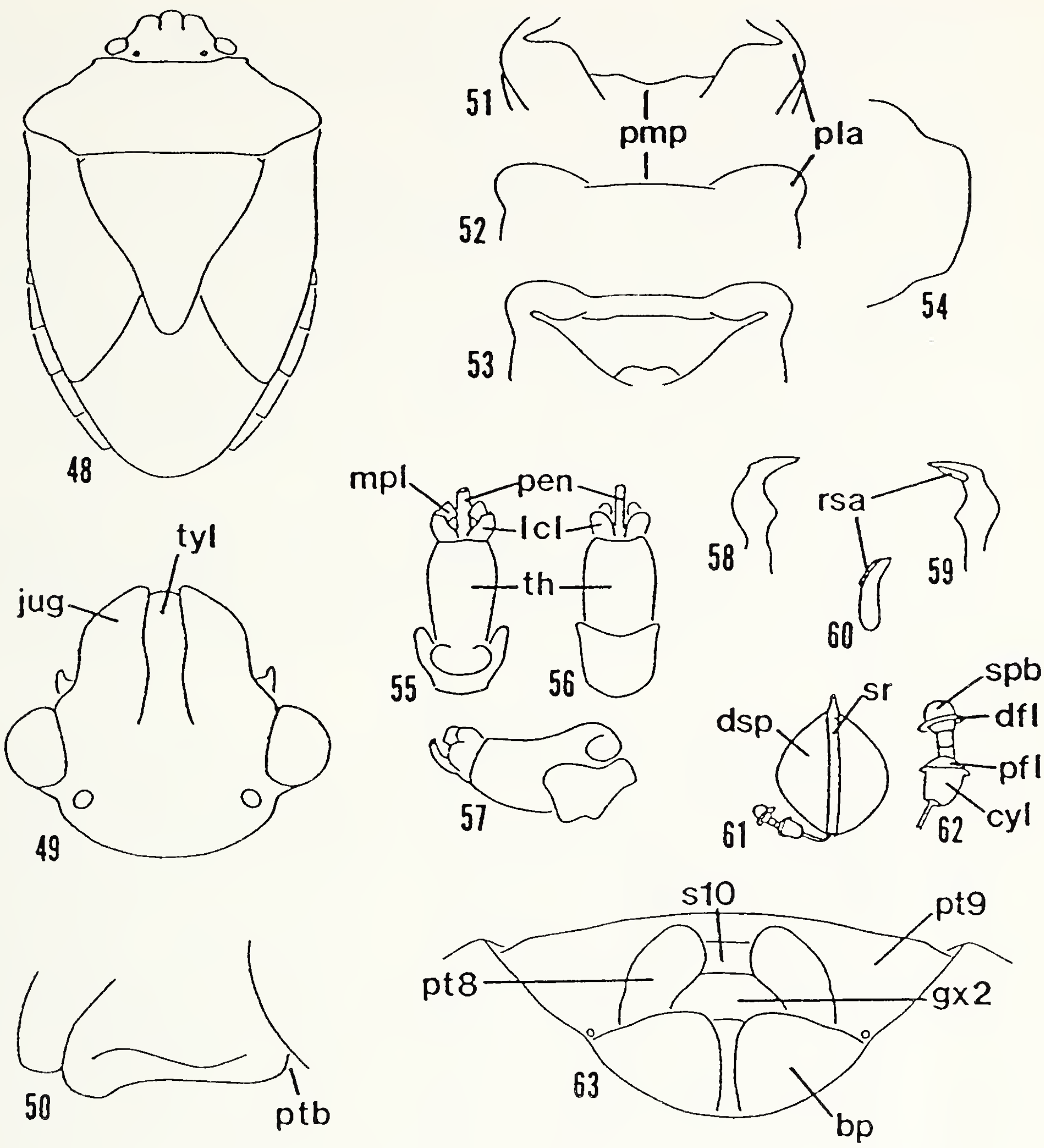
Thyanta aeruginosa Berg, 1878:24; Lethierry and Severin, 1893:147; Kirkaldy, 1909: 94; Rolston and McDonald, 1984:83–84.

Phacidium euchlorum Breddin, 1912:92–93. (syn. by Rolston and McDonald, 1984)

Diagnosis. Ovate, distinctly convex; dorsal punctation minute, dense.

Head declivitous; juga distinctly longer than tylus, outer jugal margins subparallel for middle third of distance from eyes to apex (Fig. 49). Segment 2 of each antenna at least 1.5 times as long as segment 3. Posterior termination of each buccula arcuately truncate. Anterolateral margins of pronotum weakly carinate, straight to slightly concave; each humeral angle rounded, at most protruding slightly beyond base of adjacent corium (Fig. 48); pronotal cicatrices immaculate, often slightly paler than surrounding surface. Hemelytral membranes hyaline, lacking brown flecks. Connexiva and abdominal venter lacking all black markings. Superior surface of each tibia asulcate.

Mesial and posterior margins of basal plates straight to slightly convex, posteromesial angles rounded (Fig. 63). Sclerotized rod slightly swollen subapically, narrowed



Figs. 48–63. *T. aeruginosa.* 48. Habitus. 49. Head. 50. Buccula, lateral view. 51–54. Pygophore. 51. Caudal view. 52. Ventral view. 53. Dorsal view. 54. Lateral view. 55–57. Theca and related structures. 55. Ventral view. 56. Dorsal view. 57. Lateral view. 58–60. Right paramere. 58. Medial view. 59. Lateral view. 60. Ectal view. 61. Spermatheca. 62. Spermathecal pump. 63. Genital plates, caudoventral view. Symbols: bp, basal plate; cyl, cylindrical structure below proximal flange; dfl, distal flange; dsp, dilation of spermatheca; gx2, second gonacoxa; jug, juga; lcl, lateral conjunctival lobe; mpl, median penial lobe; pen, penisfilum; pfl, proximal flange; pla, posterolateral angle of pygophore; pmp, posterior margin of pygophore; ptb, posterior termination of buccula; pt8, eighth paratergite; pt9, ninth paratergite; rsa, roughened spiculate area on lateral surface of paramere; spb, spermathecal bulb; sr, sclerotized rod; s10, tenth sternite; th, theca; tyl, tylus.

apically (Fig. 61); spermathecal bulb globose; spermathecal duct forming cylindrical structure below proximal flange (Fig. 62).

Posteroventral surface of pygophore arcuately rounded; posterior margin of pygophore sinuously U-shaped in caudal view (Fig. 51); slightly convex in lateral view (Fig. 54); posterolateral angles prominent in ventral and dorsal views (Figs. 52, 53). Apex of each paramere spinose, curving gently mediad from ectal view (Fig. 60); ectal surface convex, lacking dorsomedial concave surface (Fig. 58); roughened, spic-

ulate area on lateral surface elongate, linear (Fig. 59). Aedeagus with each lateral conjunctival lobe somewhat reduced, apices of median penial lobes visible from lateral view (Fig. 57); penisfilum well-developed (Fig. 55); theca lacking dorsolateral protuberance near caudal limit (Fig. 56).

Types. Berg (1878) described *T. aeruginosa* from at least 1♂ and 3♀♀ from Buenos Aires and Mendoza, Argentina, without designating a holotype or paratypes. The ♀ labeled (a) "Typus" (b) "Buenos Aires" (c) "1398" is designated lectotype. The remaining three specimens are designated paralectotypes. They have the following label data: (a) "Typus" (b) "Mendoza" (c) "1398" (2♀♀); and (a) "Typus" (b) "Buenos Aires" (c) "Thyanta aeruginosa Berg" (d) "1398" (♂?—abdomen missing). The lectotype and all three paralectotypes were examined, and are conserved in the Universidad Nacional de La Plata (Argentina).

Breddin (1912) described *Phacidium euchlorum* from 1♀ and 2♂♂; without designating a holotype or paratypes. Rolston and McDonald (1984) synonymized this species with *T. aeruginosa* and designated a lectotype and paralectotypes. The type specimens, which are housed in the Université Louis Pasteur, Strasbourg, France, were examined.

Distribution. Southern South America (Map 1).

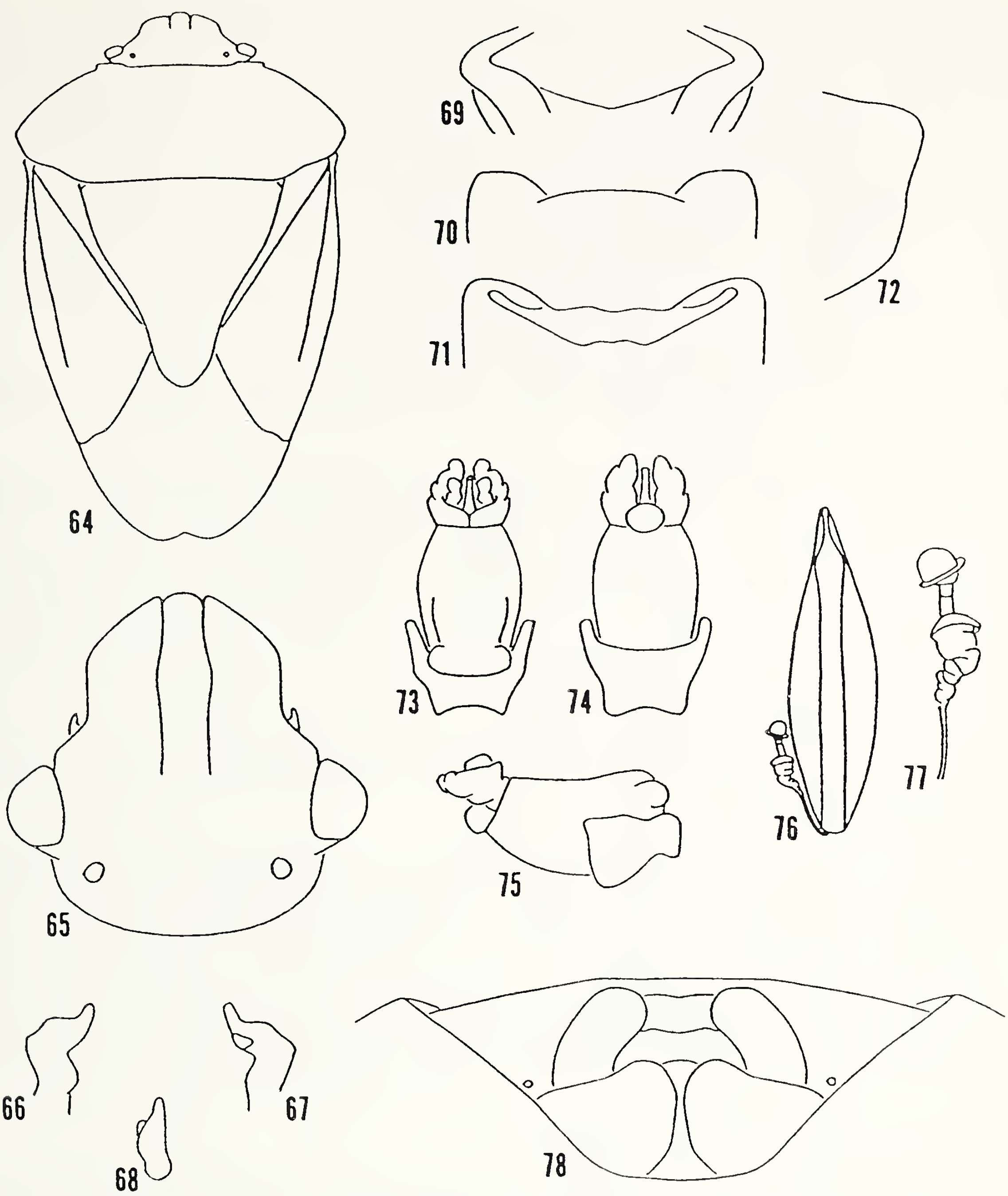
Specimens examined. 260 specimens collected between 24 September and 25 June; deposited in AMNH, BMNH, CAS, CU, DAR, LHR, MBR, MLP, SMEK, UNL, USNM, ZMB. PARAGUAY: Gran Chaco, 260 km W Paraguay R. ARGENTINA: Ibarra Grasso. *Buenos Aires:* Buenos Aires; Lujan; Punta Lara; Quesada; Santa de la Ventana; Tigre. *Catamarca. Chaco:* Resistencia. *Chubut:* Trelew. *Córdoba:* Ao. Tegua; Córdoba. *Corrientes:* Concepción. *Formosa:* Gran Guardia. *Jujuy:* Jujuy. *La Rioja:* Guandacol; 20 km N La Rioja; Los Robles. *Mendoza:* Mendoza; 100 km N Mendoza; Potrerillos; San Martin; San Rafael; 40 km N San Rafael. *Neuquéun:* Barrancas. *Río Negro:* General Fernandez Oro. *San Juan:* San Juan; 51 mi N San Juan. *San Luis:* Buena-Vista R. Batavia. *Santa Fe:* Carcaraña; Ceres; Montevideo; Santa Fe; Santa Fe River Salt Flats; Villa Ana. *Santiago del Estero:* Chaco de Santiago; Rio Salado. *Tucumán:* San Miguel de Tucumán. URUGUAY: *Colonia:* La Estanzuela. *Montevideo:* Montevideo. *San José:* Santa Luzia.

Comments. Thyanta aeruginosa can be separated from all other congeners by the asulcate tibiae, the juga which are distinctly longer than the tylus, and the second antennal segment which is distinctly longer than the third segment.

Thyanta (Phacidium) convexa Rider, new species
Figs. 64–78, Map 1

Description. General form ovate, distinctly convex. Dorsal surface stramineous to pale brown, punctures dark brown to dark green, a few interstitial pale points scattered on each corium.

Dorsal surface of head transversely convex; juga and tylus subequal in length or tylus slightly longer than juga. Outer jugal margins subparallel for middle third of distance from eyes to apex (Fig. 65). Antennae pale brown to green, segments 3–5 usually faintly darker on distal half of each segment. Anterolateral pronotal margins weakly convex in dorsal view (Fig. 64), concolorous with rest of pronotum. Humeral angles narrowly rounded, protruding slightly beyond base of adjacent coria (Fig. 64). Pronotal cicatrices immaculate. Apex of each corium narrowly rounded, usually



Figs. 64–78. *T. convexa*. 64. Habitus. 65. Head. 66–68. Right paramere. 66. Medial view. 67. Lateral view. 68. Ectal view. 69–72. Pygophore. 69. Caudal view. 70. Ventral view. 71. Dorsal view. 72. Lateral View. 73–75. Theca and related structures. 73. Ventral view. 74. Dorsal view. 75. Lateral view. 76. Spermatheca. 77. Spermathecal pump. 78. Genital plates, caudoventral view.

reaching beyond middle of penultimate connexival segment; posterior margin of corium convex; hemelytral membranes hyaline with several faint brown flecks. Connexiva pale brown, posterolateral angle of each segment usually black.

Ventral surface pale brown to green; abdominal punctures concolorous with surface; punctures on thoracic pleura usually dark brown. Posterior termination of each buccula roundly truncate. Rostrum reaching to posterior margin of third (second visible) abdominal segment. Ostiolar canal acuminate distally. Legs pale brown to green. Postspiracular black spot usually present on each side of each abdominal sternite. Posterolateral angles of abdominal sternites piceous.

Mesial margins of basal plates in caudoventral view convex; posterior margins sinuous, slightly concave, posteromesial angles rounded (Fig. 78). Sclerotized rod slightly swollen subapically, distinctly narrowed apically (Fig. 76); spermathecal duct swollen and with much coiling below proximal flange (Fig. 77). Posterior margin of pygophore in caudal view U-shaped, medial portion concave (Fig. 69); posterolateral angles prominent in ventral and dorsal views (Figs. 70, 71); posteroventral surface arcuately rounded, not produced caudad in lateral view (Figs. 72). Apex of each paramere narrowly rounded in ectal view (Fig. 68), curving distinctly dorsad in medial view (Fig. 66); roughened, spiculate area on lateral surface circular (Fig. 67). Each lateral conjuctival lobe of aedeagus with single rounded diverticulum (Fig. 73); dorsomedial conjunctival lobe distinct (Fig. 74); median penial lobes and penisfilum moderately prominent (Fig. 73).

Measurements. Total length 6.31–7.18 (6.31); total width 4.10–4.73 (4.42); medial length of pronotum 1.51–1.73 (1.51). Medial length of scutellum 2.80–3.13 (2.83); basal width 2.65–2.98 (2.87); width at distal end of frena 1.03–1.25 (1.07). Length of head 1.64–1.81 (1.64); width 2.03–2.19 (2.06). Length of segments 1–5 of antennae 0.37–0.40 (0.37), 0.70–0.81 (0.81), 0.72–0.83 (0.74), 0.98–0.99 (0.98), and 0.99–1.03 (1.03), respectively. Length of segments 2–4 of rostrum 1.21–1.42 (1.21), 0.66–0.74 (0.68), and 0.81–0.83 (0.83), respectively.

Holotype. ♂ labeled (a) "Peru S.A. III.19 1937 E.G. Smyth" (b) "J.R.de la Torre-Bueno Collection K.U." Deposited in the Snow Entomological Museum, University of Kansas (Lawrence).

Paratypes. 1♂, 7♀♀. Labeled same as holotype (2♀♀ SMEK); labeled as holotype except "III.16 1937" (♀ SMEK); labeled as holotype except "I.26 1936" (♀ SMEK); (a) "Lima(Peru) VI. 1939 leg. Weyrauch" (b) "W K W 5776" (♂ USNM); "Peru. Dpto. Amazonas 43 K. ne. Chikiaco 1050′ 6–10 XI 1978 L. J. Barkley" (♀ LHR); (a) "PERU:8 km. NE. Pucusana, Lima. IX-12-54" (b) "E.I.Schlinger & E.S.Ross collectors" (♀ CAS); (a) "PERU Chancay river valley III-15-51" (b) "Ross and Michelbacher Collectors" (♀ CAS); (a) "ECUADOR Guayaquil" (b) "12-1-53 at light" (♀ USNM).

Distribution. Ecuador and Peru (Map 1).

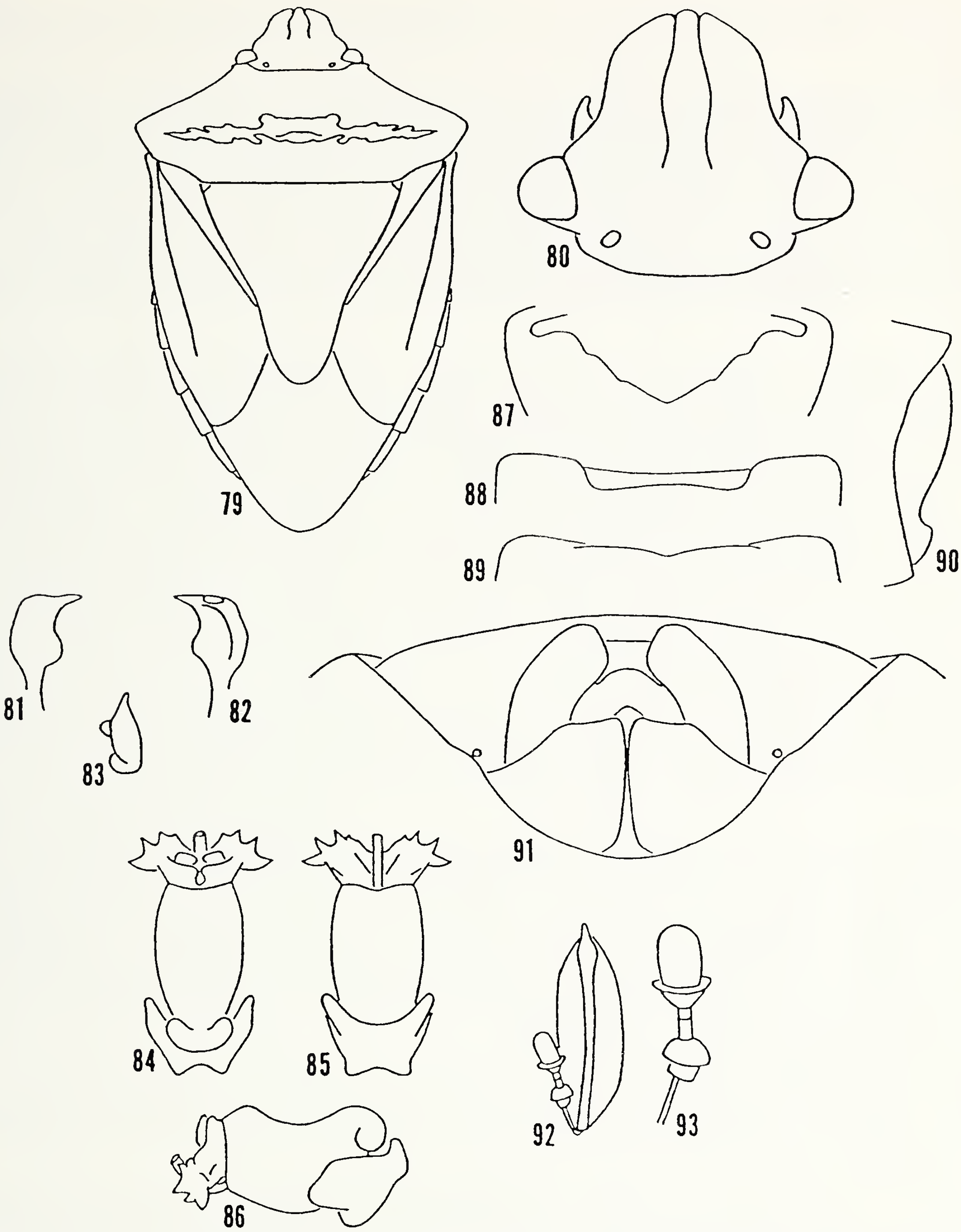
Comments. Thyanta convexa and *T. aeruginosa* are very similar in general appearance and are the only two species in the genus that have the posterior termination of each buccula roundly truncate; in all other species it is evanescent. *Thyanta convexa* differs from *T. aeruginosa* in having the superior surface of each tibia sulcate and the juga and tylus subequal in length. *Thyanta convexa* further differs from all other congeners by the slightly convex anterolateral pronotal margins and the male genitalia.

Etymology. Named for the convex anterolateral margins of the pronotum.

Thyanta (Phacidium) fimbriata Rider, new species
Figs. 79–93, Map 4

Description. Dorsal surface brown to medium green; usually anterior disc of pronotum paler than posterior disc.

Head evenly rounded apically; outer jugal margins sinuous, not parallel (Fig. 80). Antennae green to brown, distal third of segment 3 reddish-brown, segments 4–5 entirely reddish brown. Anterolateral margins of pronotum in dorsal view concave;



Figs. 79–93. *T. fimbriata.* 79. Habitus. 80. Head. 81–83. Right paramere. 81. Medial view. 82. Lateral view. 83. Ectal view. 84–86. Theca and related structures. 84. Ventral view. 85. Dorsal view. 86. Lateral view. 87–90. Pygophore. 87. Caudal view. 88. Ventral view. 89. Dorsal view. 90. Lateral view. 91. Genital plates, caudoventral view. 92. Spermatheca. 93. Spermathecal pump.

each humeral angle narrowly rounded to angulate, protruding beyond base of adjacent corium (Fig. 79). Each pronotal cicatrice marked with piceous in mesial angle. Usually an elevated, pale, subcalloused line present between humeral angles. Hemelytra uniformly punctate, lateral margin at base pale, subcalloused; posterior margins convex (Fig. 79); costal angle rounded, usually reaching to near middle of penultimate connexival segment; hemelytral membranes hyaline with few to many pale brown flecks.

Connexiva narrowly exposed, brown to green; posterolateral angle of each segment piceous.

Ventral surface pale to medium brown, rarely with small dark-brown spots scattered on abdomen. Rostrum pale brown, most of segment 4 black, apex reaching between metacoxae or slightly beyond. Ostiolar canal acuminate apically. Femora and tibiae pale brown to green with fuscous spot on superior surface of each femur at distal third, rarely with scattered small brown spots; tarsal segments reddish or dark brown. Postspiracular black spot usually present on each side of each abdominal sternite; posterolateral angles of each sternite piceous, anterolateral angles immaculate.

Basal plates in caudoventral view subtriangular; mesial margins slightly convex; posterior margins sinuous, posteromesial angles narrowly rounded (Fig. 91). Sclerotized rod swollen subapically, narrowed apically (Fig. 92); spermathecal duct swollen, forming small cylindrical structure below proximal flange (Fig. 93). Posteroventral surface of pygophore deeply sulcate, becoming shallow laterally, obtuse carina below sulcus bearing row of long setae; posterior margin of pygophore sinuously V-shaped in caudal view, also bearing row of setae (Fig. 87); pygophore shallowly concave in both ventral and dorsal views (Figs. 88, 89); in lateral view, broadly convex with emargination ventrally (Fig. 90). Each paramere robust, apex spinose in both medial and ectal views (Figs. 81, 83); roughened, spiculate area on lateral surface circular (Fig. 82). Each lateral conjunctival lobe of aedeagus with 3–4 spinose diverticula (Fig. 84); dorsomedial conjunctival lobe apparently absent (Fig. 85); penisfilum prominent (Fig. 85); median penial lobes relatively small (Fig. 84).

Measurements. Total length 6.47–8.44 (8.04); total width 4.49–5.91 (5.60); medial length of pronotum 1.55–1.84 (1.84). Medial length of scutellum 2.80–3.72 (3.39); basal width 2.72–3.39 (3.16); width at distal end of frena 1.07–1.40 (1.40). Length of head 1.44–1.68 (1.68); width 1.88–2.21 (2.12). Length of segments 1–5 of antennae 0.35–0.42 (0.42), 0.74–0.81 (0.79), 0.72–0.96 (0.96), 0.94–1.18 (1.18), and 0.74–1.18 (1.18), respectively. Length of segments 2–4 of rostrum 1.16–1.34 (1.34), 0.70–0.77 (0.70), and 0.66–0.81 (0.81), respectively.

Holotype. ♂ labeled "BRAZIL, Sao Paulo: Serra da Bocaina S.Jose Barreiro 1650 m., Jan. 1969 M. Alvarenga." Deposited in the American Museum of Natural History (New York).

Paratypes. 3♂♂, 2♀♀. "São Paulo Campos do Jordão 16.XII.1944. F. Lane col." (♂ MZRS); (a) "Curitiba-Pr. IX-1960 R.Lange leg." (b) "Lange" (♂ MAPA); (a) "Porto Alegre 11.10.50" (b) "Rio Grande do Sul, Pe. Buck leg." (♀ MAPA); (a) "Jordao R Parana Braz. 12 II 52" (b) "C J Drake Coll. 1956" (♂ USNM); and (a) "Jello 1." (b) "Z.M.B. Hem." (♀ ZMB).

Distribution. Southern Brazil (Map 4).

Comments. The distinct sulcus on the posteroventral surface of the pygophore and the double row of long setae are unique within the genus. The cylindrical structure below the proximal flange of the spermatheca is unique within this subgenus.

Etymology. Named for the double row of long hairs on the pygophore.

Thyanta (*Phacidium*) *juvenca* Stål
Figs. 94–108, Map 4

Thyanta juvenca Stål, 1862b:104; Stål, 1872:35; Lethierry and Severin, 1893:148; Berg, 1900:89; Kirkaldy, 1909:94; Jensen-Haarup, 1928:189.

Euschistus juvencus: Walker, 1867:247.
Pentatoma pilosum Reed, 1898:132. (syn. by Kirkaldy, 1909)

Diagnosis. Medium-sized; slightly convex dorsally, distinctly convex ventrally. Dorsal surface pale to medium green, usually with yellow or red markings on apex of tylus, on apex of scutellum, on each humeral angle, and on legs.

Apex of head narrowly rounded; outer jugal margins sinuous, not parallel (Fig. 95). Anterolateral margins of pronotum straight to slightly concave in dorsal view; humeral angles obtusely to narrowly rounded, protruding only slightly beyond base of adjacent coria (Fig. 94). Each pronotal cicatrice usually immaculate, sometimes marked with black in mesial angle.

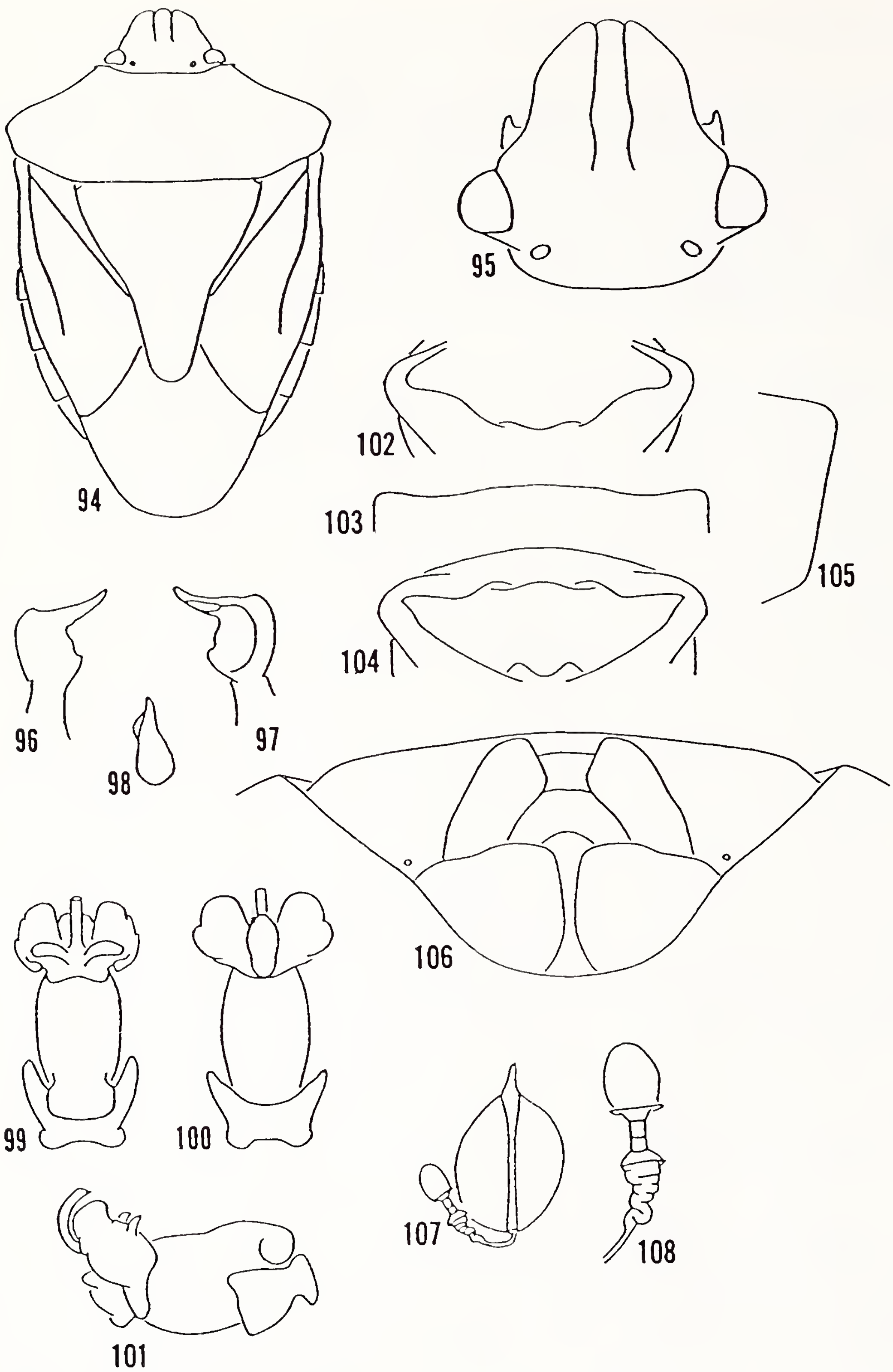
Mesial margins of basal plates in caudoventral view straight to slightly convex; posterior margins sinuously convex; posteromesial angles rounded (Fig. 106). Sclerotized rod relatively short, swollen subapically; narrowed apically (Fig. 107); spermathecal duct with large amount of swelling and coiling below proximal flange (Fig. 108). Posterior margin of pygophore shallowly and sinuously U-shaped in caudal view (Fig. 102); posteroventral surface of pygophore straight in lateral view (Fig. 105); slightly convex in ventral and dorsal views (Figs. 103, 104). Each paramere robust; apex spinose, curved gently laterad in ectal view (Fig. 98), curving gently dorsad in medial view (Fig. 96); shaft with nearly angulate protuberance at middle; roughened, spiculate area on lateral surface linear (Fig. 97). Each lateral conjunctival lobe of aedeagus with single rounded diverticulum (Fig. 101); dorsomedial conjunctival lobe moderately large (Fig. 100) penisfilum prominent, median penial lobes small, inconspicuous (Fig. 99).

Types. Stål (1862b) described *T. juvenca* from 1♂ from Chile. In the original description, he states that the type specimen was placed in the "Mus. Helsingfors" in Finland. The type specimen was not located in the Universitetets Zoologiske Museum (Helsingfors, Finland). However, the original description is adequate to fix the species. In his description, Stål says "Thorax marginibus lateralibus anticis integris, levissime sinuatis, angulis lateralibus obtusus, vix prominulis." Only three species of *Thyanta* are known to occur in Chile: *T. juvenca, T. xerotica* and *T. rubicunda. Thyanta xerotica* is relatively rare and occurs only in the very northern areas of Chile. *Thyanta rubicunda* has each humeral angle produced into an acute spine. *Thyanta juvenca* is the only common and widespread species in Chile that has each humeral angle obtusely rounded as in the above description.

Reed (1898) described *Pentatoma pilosum* from 2♂♂ from Chile without designating a holotype. The ♂ labeled (a) "Sin. Hem. Chile Coll. EC Reed" (b) "CJ Drake Coll. 1956" is designated lectotype. The ♂ labeled (a) "Sin. Hem. Chile Coll. ECReed" (b) "C J Drake Coll. 1956" (c) "Pent. spe nov." (d) "*juvenca*" (e) "*Thyanta*" is designated paralectotype. Kirkaldy (1909) properly placed this species as a junior synonym of *T. juvenca.* Both specimens were examined and are housed in the U.S. National Museum of Natural History (Washington, D.C.).

Distribution. Chile (Map 4).

Specimens examined. 79 specimens collected from 7 September to 17 May; deposited in AMNH, CAS, CNC, DAR, EGER, ENGL, FSCA, LHR, MNHS, UCR, UCS, USNM, ZMB. CHILE: *Atacama:* Río Manflas. *Bíbío:* Arauco; Queime, E. Concepción. *Coquimbo:* Rivadavia; Vicuña. *El Liberatador General Bernardo O'Higgins:* Rancagua; 10 km N San Fernando; San Vicente de Tauga. *Maule:* Cauquenes; La Jaula. Cord. Curicó; coast nr. Mataquito R. *Región Metropolitana de Santiago:*



Figs. 94–108. *T. juvenca.* 94. Habitus. 95. Head. 96–98. Right paramere. 96. Medial view. 97. Lateral view. 98. Ectal view. 99–101. Theca and related structures. 99. Ventral view. 100. Dorsal view. 101. Lateral view. 102–105. Pygophore. 102. Caudal view. 103. Ventral view. 104. Dorsal view. 105. Lateral view. 106. Genital plates, caudoventral view. 107. Spermatheca. 108. Spermathecal pump.

Buin; Co San Ramon; Clovillo; Curacaví; El Canelo; La Matancilla; Los Maitenes; Melocoton; Quebrada Macul; Quilicura; Rinconada Maipú; San Bernardino; Santiago. *Tarapacá:* Arica. *Valparaíso:* La Cruz; Los Andes; Ocoa; Papudo.

Comments. Thyanta juvenca is closely related to *T. acutangula,* which may actually

be a subspecies of the former. The male genitalia of the two species are nearly identical. *Thyanta juvenca* has each humeral angle obtusely rounded, while in *T. acutangula* each humeral angle is distinctly angulate.

Thyanta (Phacidium) acutangula Jensen-Haarup
Figs. 109–123, Map 4

Thyanta acutangula Jensen-Haarup, 1928:189, 190–191.
Thyanta mendozana Jensen-Haarup, 1928:189, 190. NEW SYNONYMY.
Thyanta crinita Ruckes, 1957b:44–46. NEW SYNONYMY.

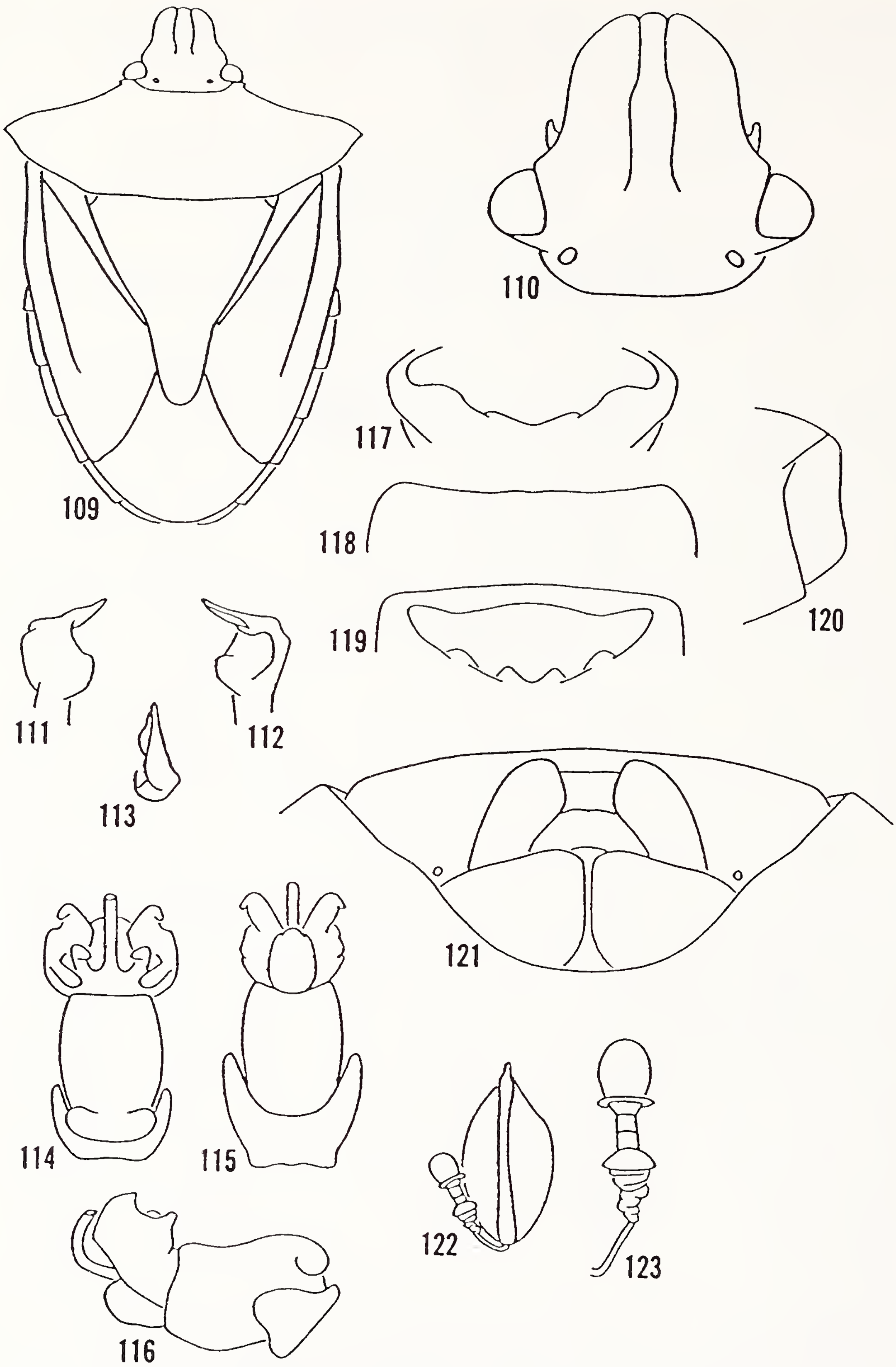
Diagnosis. Medium-sized; ovate. Dorsal surface pale brown to dark green, sometimes dark brown, often marked with yellow around pronotal cicatrices, along anterolateral margins of pronotum, and on apex of scutellum; punctures usually concolorous with surface, sometimes brown.

Head evenly rounded apically; outer jugal margins sinuous, nearly parallel for middle third of distance from eyes to apex (Fig. 110). Anterolateral margins of pronotum slightly concave in dorsal view; humeral angles angulate to spinose, flaring dorsad and slightly caudad, apices usually piceous (Fig. 109). Pronotal cicatrices immaculate or sometimes marked with black in mesial angles.

Mesial margins of basal plates in caudoventral view straight to slightly convex; posterior margins convex; posteromesial angles rounded (Fig. 121). Sclerotized rod slightly swollen subapically, narrowed but not elongate apically (Fig. 122); spermathecal duct swollen and coiled below proximal flange (Fig. 123). Posteroventral surface of pygophore rounded; posterior margin sinuously U-shaped in caudal view, medial portion concave (Fig. 117). Posterior margin of pygophore nearly straight in ventral view (Fig. 118); slightly convex in dorsal view, posterolateral angles not at all prominent (Fig. 119); straight to weakly concave in lateral view (Fig. 120). Each paramere robust, acuminately spinose in medial and ectal views (Figs. 111, 113); roughened spiculate area on lateral surface narrow, elongate (Fig. 112). Each lateral conjunctival lobe of aedeagus spinose apically and with rounded, partially sclerotized diverticulum ventrally (Fig. 114); dorsomedial conjunctival lobe present (Fig. 115); median penial lobes hooked; penisfilum large, elongate, curving ventrad (Fig. 116).

Types. Jensen-Haarup (1928) described *T. acutangula* from 3♂♂ and 3♀♀ all from Mendoza Province in Argentina. He did not, however, designate a holotype or paratypes. The ♂ labeled (a) "Est. Pedregal Prov. de Mendoza Rep. Argentina J.-Hrp." (b) "Type Coll. J=Hrp." (c) "Coll. Jensen-Haarup" (d) "Thyanta acutangula Jensen-Haarup leg." is designated lectotype. The remaining five specimens are designated paralectotypes. They have the following label data: (a) "Mendoza" (b) "Coll. Jensen-Haarup" (c) "Type Coll. J=Hrp." (d) "Thyanta acutangula Jensen-Haarup leg" (♂); (a) "Mendoza 25.3.08" (b) "Type Coll. J=Hrp." (c) "Coll. Jensen-Haarup" (d) "Thyanta acutangula Jensen-Haarup leg" (♂); labeled as lectotype except (b) and (c) are reversed and (d) "Thyanta acutangula J-Hrp. Coll. Jensen-Haarup" (♀); (a) "Chacr. de Coria Prov. de Mendoza Rep. Argentina Jensen-Haarup" (b) "Type Coll. J=Hrp." (c) "Type" (d) "Thyanta acutangula Jensen-Haarup leg." (♀); and (a) "Mendoza 12.4.07" (b) "Type Coll. J=Hrp." (c) "Type" (d) "Thyanta acutangula n. sp. J-Hrp." (♀). All six specimens were examined and are conserved in the Universitetets Zoologiske Museum (Copenhagen, Denmark).

Jensen-Haarup (1928) described *T. mendozana* from 1♂ from the province of



Figs. 109–123. *T. acutangula.* 109. Habitus. 110. Head. 111–113. Right paramere. 111. Medial view. 112. Lateral view. 113. Ectal view. 114–116. Theca and related structures. 114. Ventral view. 115. Dorsal view. 116. Lateral view. 117–120. Pygophore. 117. Caudal view. 118. Ventral view. 119. Dorsal view. 120. Lateral view. 121. Genital plates, caudoventral view. 122. Spermatheca. 123. Spermathecal pump.

Mendoza, Argentina. The holotype is of the brown form and is slightly teneral, making some characters hard to distinguish. Although the holotype has the humeral angles obtusely rounded, it does have fuscous markings on the ventral surface of each humeral angle, a trait characteristic of *T. acutangula.* Its male genitalia are virtually indistinguishable from those of *T. acutangula.* The holotype was examined and is housed in the Universitetets Zoologiske Museum (Copenhagen, Denmark).

Ruckes (1957b) described *T. crinita* from 1♂ and 2♀♀ from Argentina. The holotype and one paratype were examined, and they do not differ in any significant respect from *T. acutangula.* These specimens are housed in the Cornell University collection (New York).

Distribution. Western Argentina (Map 4).

Specimens examined. 135 specimens collected from 6 January to 5 April; deposited in AMNH, CAS, CU, EGER, IML, LHR, MBR, MLP, PUL, USNM, ZMB. BOLIVIA: *Chuquisaca:* Muyupampa. *Cochabamba;* 30 mi SW Cochabamba. *La Paz:* Sorata. *Mataral:* Santa Rosa. ARGENTINA: *Catamarca:* Belén; El Rodeo. *Chubut:* Altares; Puerto Madryn. *Córdoba:* Alta Garcia; 5 mi N Deán Funes; Guanaco Muerto. *La Pampa:* Lihuel Calel; Puelén. *La Rioja. Mendoza:* Chacr. de Coria; El Sosneado; Est. Pedregal; Portrerillos. *Neuquén:* Barrancas. *Río Negro:* Choele-Choel; General Fernández Oro; San Antonio Oeste; Villa Regina. *Salta:* Cafayate; Cnel. Moldes; Metan; San Lorenzo. *San Luis:* Beasley; San Luis; San Martín. *Tucumán:* Amaicha del Valle; Crest ridge, NW Tucumán; Quebrada de Lules; Río Calchuquier.

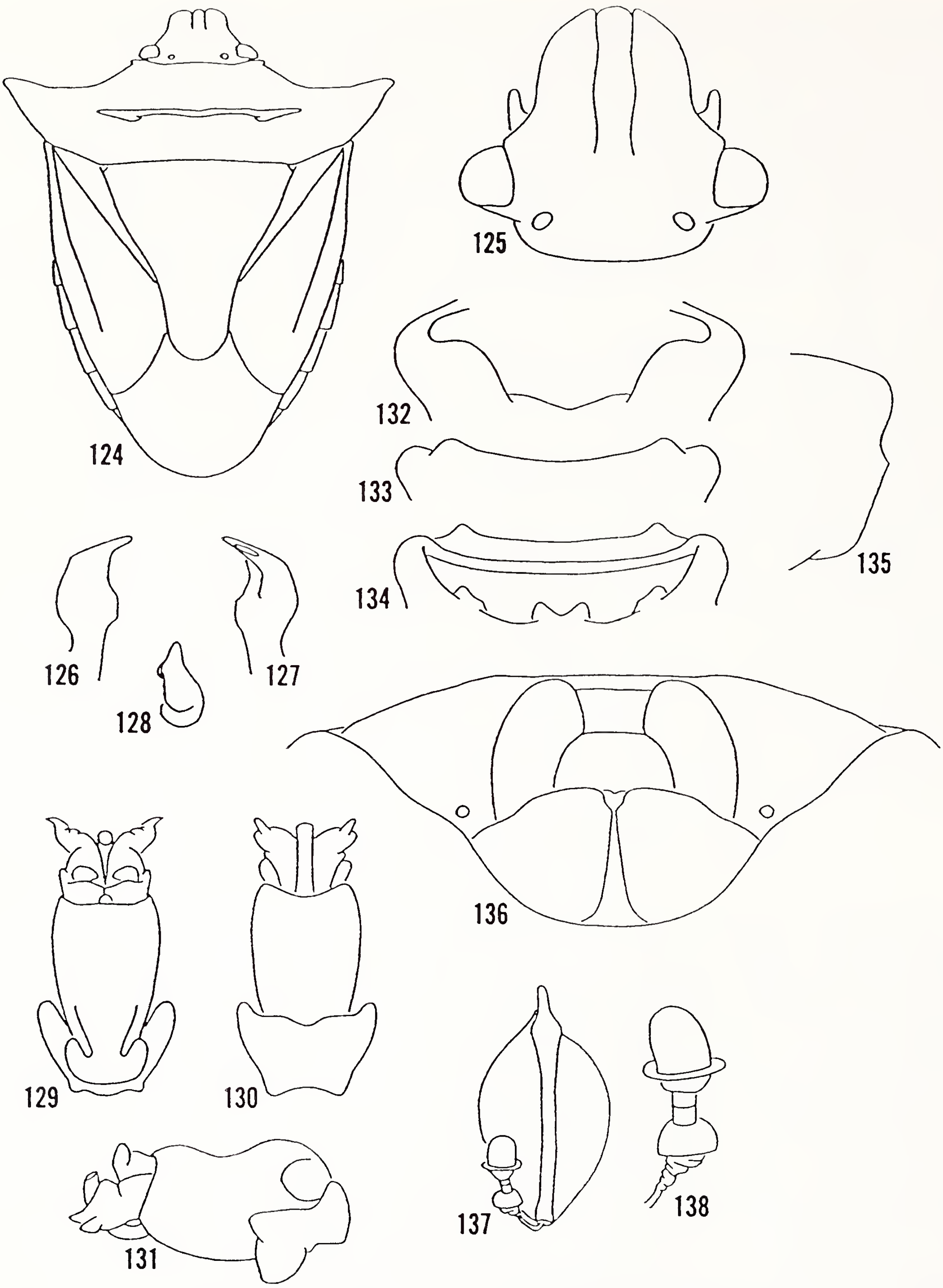
Comments. This species is related to *T. juvenca,* and may actually be a subspecies of that species. The genitalia of the two species are nearly identical. *Thyanta acutangula* can be separated from *T. juvenca* by the angulate to spinose humeral angles.

Thyanta (Phacidium) robusta Rider, new species
Figs. 124–138, Map 4

Description. Medium to large; dorsal surface dusky brown to greenish brown; broadly ovate, robust. Punctures brown, usually becoming fuscous near each humeral angle and in irregular band just posterior to transhumeral pale subcalloused line.

Apex of head evenly rounded; outer jugal margins nearly parallel for middle third of distance from eyes to apex (Fig. 125). Antennae brown, segments 1–2 sometimes vaguely marked with fuscous, segments 3–5 often reddish. Anterolateral margins of pronotum concave in dorsal view; humeral angles produced anterolaterad and dorsad, spinose (Fig. 124). Mesial angle of each pronotal cicatrice marked with fuscous, sometimes only vaguely so. A raised transhumeral subcalloused line usually present. Disc of pronotum anterior to cicatrices depressed, punctures crowded, small. Hemelytra with exocorium of each more densely punctate than rest of corium; posterior margin of corium convex, costal angle narrowly rounded, usually reaching beyond middle of penultimate connexival segment (Fig. 124); hemelytral membranes hyaline with numerous fuscous flecks. Connexiva green to brown, posterolateral angles black, sometimes posterior margin of each segment marked with fuscous.

Ventral surface pale brown to green; punctures usually concolorous with surface, sometimes pale brown. Rostrum pale brown to green, apical half of segment 4 piceous, reaching to anterior margin of third (second visible) abdominal sternite. Ostiolar canals acuminate apically. Humeral angles often piceous. Femora and tibiae pale brown, tarsal segments darker, reddish; femora sometimes marked with a few pale



Figs. 124–138. *T. robusta.* 124. Habitus. 125. Head. 126–128. Right paramere. 126. Medial view. 127. Lateral view. 128. Ectal view. 129–131. Theca and related structures. 129. Ventral view. 130. Dorsal view. 131. Lateral view. 132–135. Pygophore. 132. Caudal view. 133. Ventral view. 134. Dorsal view. 135. Lateral view. 136. Genital plates, caudoventral view. 137. Spermatheca. 138. Spermathecal pump.

brown spots, usually one dark brown to fuscous spot on superior surface at distal third. Postspiracular black spot usually present on each side of each abdominal sternite; posterolateral angle of each abdominal sternite piceous.

Mesial margins of basal plates in caudoventral view nearly straight; posterior margins sinuously convex; posteromesial angles weakly emarginate (Fig. 136). Sclerotized rod swollen subapically, distinctly narrowed apically (Fig. 137); spermathecal duct slightly swollen and coiled below proximal flange (Fig. 138). Posteroventral surface of pygophore arcuately rounded; posterior margin in caudal view U-shaped, medial portion concave (Fig. 132). Pygophore in lateral view emarginate on dorsal half (Fig. 135); each lateral angle appearing double-cone-shaped in both ventral and dorsal views (Figs. 133, 134). Each paramere robust, apex nearly spinose in medial view (Fig. 126); apex narrowly rounded, curved slightly mediad in ectal view (Fig. 128); roughened, spiculate area on lateral surface linear, short (Fig. 127). Each lateral conjunctival lobe of aedeagus with 1–2 diverticula (Fig. 131); dorsomedial conjunctival lobe apparently absent (Fig. 130); penisfilum and median penial lobes prominent (Fig. 129).

Measurements. Total length 7.41–9.78 (7.41); total width 6.47–8.04 (6.47); medial length of pronotum 1.71–1.99 (1.71). Medial length of scutellum 3.31–4.08 (3.40); basal width 3.20–3.84 (3.28); width at distal end of frena 1.21–1.66 (1.40). Length of head 1.62–1.81 (1.62); width 2.08–2.36 (2.12). Length of segments 1–5 of antennae 0.40–0.52 (0.40), 0.81–0.94 (0.81), 1.07–1.20 (1.07), 1.14–1.25 (1.14), and 1.16–1.21 (1.21), respectively. Length of segments 2–4 of rostrum 1.25–1.62 (1.25), 0.74–0.81 (0.74), and 0.77–0.96, respectively.

Holotype. ♂ labeled "ANA RECK (MUN. CAXIAS DO SUL R. S. 9-IV-55, BRASIL E. W. GRUMAN leg." Deposited in the Florida State Collection of Arthropods (Gainesville).

Paratypes. 2♂♂, 5♀♀. Labeled same as holotype (♂ FSCA); (a) "SAO PAULO Br., Mráz" (b) "Z.M.B. Hem." (♂ ZMB); (a) "Gramado, R.G. do Sul, Brasil 6-I-50 J. Becker 123" (b) "Thyanta det RISailer" (c) "Thyanta acuta Ruckes varietal form" (d) "Compared with type. Much more robust. H. Ruckes" (♀ USNM); "GRAMADO 2. 1954 RGS BRASIL" (♀ MZRS); "Brazil, Paraná 30 mi. W Irati 23 FEB 1980 D.B. Thomas Coll." (♀ DBT); (a) "Tasimbé 24 II 57" (b) "218" (♀ MZRS); and (a) "Pinheinal 28 I 53" (b) "217" (♀ MZRS).

Distribution. Brazil (Map 4).

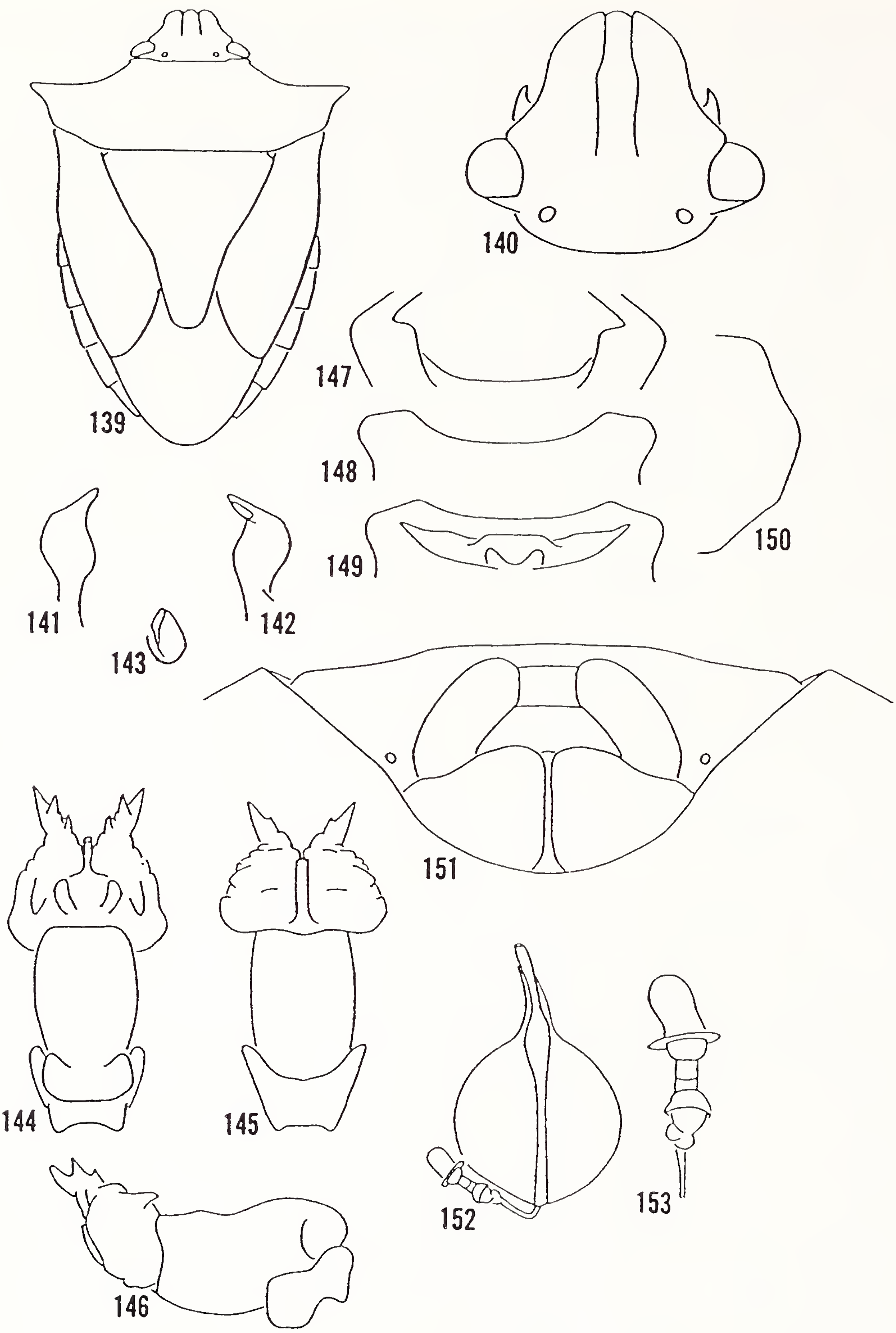
Comments. This is a fairly distinctive species, although it is closely related to *T. acuta* and *T. cornuta.* It can be separated from these species by the larger, more robust shape, and by the characters of the male genitalia. The double-cone-shaped posterolateral angles of the pygophore in ventral and dorsal views will separate this species from both *T. acuta* and *T. cornuta.*

Etymology. Named for the robust form of the humeral angles.

Thyanta (*Phacidium*) *acuta* Ruckes
Fig. 139–153, Map 4

Thyanta acuta Ruckes, 1952:67–68.

Diagnosis. Medium-sized; ovate. Dorsal surface green to dark brown, sometimes with the following structures reddish: two spots on posterior disc of pronotum, one



Figs. 139–153. *T. acuta.* 139. Habitus. 140. Head. 141–143. Right paramere. 141. Medial view. 142. Lateral view. 143. Ectal view. 144–146. Theca and related structures. 144. Ventral view. 145. Dorsal view. 146. Lateral view. 147–150. Pygophore. 147. Caudal view. 148. Ventral view. 149. Dorsal view. 150. Lateral view. 151. Genital plates, caudoventral view. 152. Spermatheca. 153. Spermathecal pump.

on each side of middle, extending to include nearly entire dorsal surface of pronotum; dorsal surface of head; marginal band on scutellum along each frenum; and all of hemelytra except exocorium.

Apex of head evenly rounded; outer jugal margins sinuous, not parallel (Fig. 140). Anterolateral margins of pronotum concave in dorsal view; humeral angles produced primarily laterad and only slightly anterodorsad, spinose (Fig. 139). Mesial angle of each pronotal cicatrice piceous; transhumeral subcalloused line usually present.

Mesial margins of basal plates in caudoventral view nearly straight; posterior margins sinous; posteromesial angles rounded (Fig. 151). Sclerotized rod swollen at about two-thirds distance from base, apical, narrowed portion elongate (Fig. 152); spermathecal bulb globose, slightly elongate, small amount of coiling of spermathecal duct below proximal flange (Fig. 153). Posteroventral surface of pygophore arcuately rounded; posterior margin in caudal view U-shaped, medial portion slightly concave (Fig. 147); pygophore in lateral view nearly arcuately convex (Fig. 150). Each paramere rather robust, apex nearly spinose in medial view (Fig. 141); blunt, robust in ectal view (Fig. 143); roughened, spiculate area on lateral surface slightly elongate (Fig. 142). Each lateral conjunctival lobe of aedeagus with 3–4 spinose diverticula apically (Fig. 146) and 1 hooked sclerotized diverticulum ventrally (Fig. 144); penisfilum large, dorsomedial conjunctival lobe apparently absent (Fig. 145).

Types. Ruckes (1952) described *T. acuta* from 1♂ and 1♀ from Paraguay. Although he described this species under the name *T. acuta,* the name placed on the label with the specimens is *T. acutissimus.* The remaining label information, however, matches exactly that given in the original description, and the specimens fit the description for *T. acuta.* The holotype was examined and is housed at the University of Michigan Museum (Ann Arbor).

Distribution. Southern South America (Map 4).

Specimens examined. 41 specimens collected from 2 September to 1 April; deposited in AMNH, CNC, LHR, MBR, MLP, USNM, ZMB. BOLIVIA: *El Beni:* Trinidad. *La Paz:* Apolo. *Santa Cruz:* Santa Cruz. BRAZIL: Raco. *Mato Grosso:* Cuiabá. *Mato Grosso do Sul:* Corumbá; Salobra. *Minas Gerais:* 60 km W Araxá. *Santa Catarina:* Nova Teutônia. *São Paulo:* Teodoro Sampaio. PARAGUAY: *Caaguazú:* Estancia Primera. *Central:* Lago Yloycaraiy, N of San Bernardino. *Concepción:* Horqueta. *Cordillera:* Caacupé. *Guaira:* Villarrica. ARGENTINA: *Misiones:* Igazú; Leandre Alem; San Ignacio; Victoria.

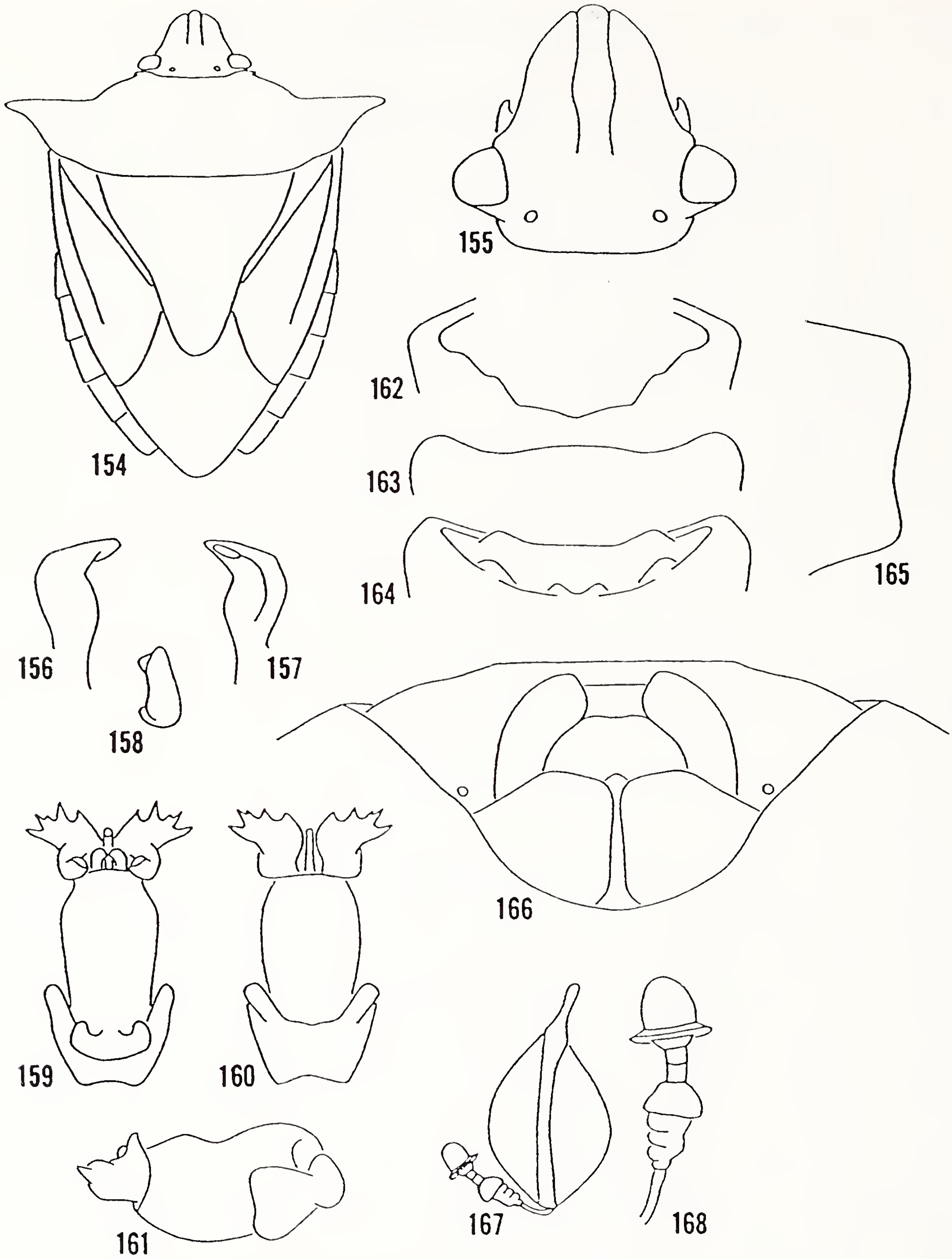
Comments. This species is closely related to *T. robusta* and *T. cornuta.* It can be separated from *T. robusta* by the less robust form and by the form of the posterolateral angles of the pygophore, which are not double-cone-shaped when viewed ventrally or dorsally. The posterior margin of the pygophore in caudal view is U-shaped in *T. acuta* and V-shaped in *T. cornuta.*

Thyanta (*Phacidium*) *cornuta* Ruckes
Figs. 154–168, Map 4

Thyanta cornuta Ruckes, 1956:66–68.

Diagnosis. Small to medium; ovate. Dorsal surface olivaceous green; punctures pale brown, sometimes reddish on pronotum and hemelytra.

Outer jugal margins sinuous, not parallel; apex of head narrowly rounded (Fig.



Figs. 154–168. *T. cornuta.* 154. Habitus. 155. Head. 156–158. Right paramere. 156. Medial view. 157. Lateral view. 158. Ectal view. 159–161. Theca and related structures. 159. Ventral view. 160. Dorsal view. 161. Lateral view. 162–165. Pygophore. 162. Caudal view. 163. Ventral view. 164. Dorsal view. 165. Lateral view. 166. Genital plates, caudoventral view. 167. Spermatheca. 168. Spermathecal pump.

155). Anterolateral margins of pronotum angularly concave in dorsal view; humeral angles produced primarily laterad and slightly anterodorsad, spinose (Fig. 154). Pronotal cicatrices usually immaculate, sometimes vaguely marked with fuscous in each mesial angle; subcalloused line between humeral angles lacking.

Mesial margins of basal plates in caudoventral view nearly straight; posterior margins sinuously convex; posteromesial angles broadly rounded (Fig. 166). Sclerotized rod relatively short, swollen subapically, narrowed apical portion elongate (Fig. 167); spermathecal duct swollen and coiled below proximal flange (Fig. 168). Posteroventral surface of pygophore arcuately rounded; posterior margin in caudal view sinuously V-shaped, lateral margins distinctly divergent (Fig. 162). Pygophore in lateral view nearly straight to slightly concave (Fig. 165); in ventral view, lateral angles slightly prominent, medial portion slightly convex (Fig. 163). Each paramere robust, apex nearly spinose in medial view (Fig. 156); rounded in ectal view (Fig. 158); roughened spiculate area on lateral surface linear, short, near apex (Fig. 157). Each lateral conjunctival lobe of aedeagus with 4–5 spinose diverticula apically and 1 slightly sclerotized diverticulum ventrally (Fig. 159); dorsomedial conjunctival lobe apparently absent (Fig. 160); median penial lobes relatively small, penisfilum moderately large (Fig. 160).

Types. Ruckes (1956) described *T. cornuta* from 1♂ and 2♀♀ from Brazil. Because the ♂ specimen was missing the pygophore, he designated one of the ♀ specimens holotype. All three specimens were examined and are housed in the American Museum of Natural History (New York).

Distribution. Northern and central South America (Map 4).

Specimens examined. Eight specimens collected in January, June, July, September, and November, deposited in AMNH, UCV. VENEZUELA: *Bolívar:* San Cayetano. BOLIVIA: *El Beni:* Río Iténez opposite Costa Marques, Brazil. BRAZIL: Chavantina. *Mato Grosso:* Chapada.

Comments. This species is closely related to *T. acuta* and *T. robusta.* It can be separated from those species by the more acuminate humeral angles, and by the characters of the male genitalia. *Thyanta acuta* has the posterior margin of the pygophore U-shaped with the sides nearly vertical. The posterior margin of *T. cornuta* is sinuously V-shaped with the sides not at all approaching the vertical axis of the body. *Thyanta robusta* has the posterolateral angles double-cone-shaped in ventral and dorsal views; *T. cornuta* does not.

Subgenus **Argosoma** Rider, new subgenus

Type species. Pentatoma patruelis Stål, 1859.

Diagnosis. Punctation coarse, sparse, dorsal surface appearing shiny, glossy. Anterolateral margins of pronotum straight to slightly concave, concolorous with surface of pronotum; humeral angles rounded to angulate, rarely spinose; pronotal cicatrices usually immaculate, sometimes faintly marked with fuscous in mesial angles. Posterior termination of each buccula evanescent.

Distal end of sclerotized rod with or without subapical swelling, never cone-shaped; spermathecal bulb globose; spermathecal duct below proximal flange slightly to greatly swollen and coiled, but never forming distinct cylindrical structure. Pygophoral opening relatively large; posterior margin usually broadly and shallowly U-shaped; posteroventral surface of pygophore produced into blunt chin-like protuberance. Each paramere acute to narrowly rounded apically, obtuse protuberance on shaft moderate in size to absent, possessing distinct dorsomedial concave surface; roughened, spiculate area on lateral surface of paramere usually circular, rarely linear (*T. boliviensis*). Theca reniform, lacking dorsolateral protuberances; each lateral conjunctival lobe

usually with single diverticulum; median penial lobes and penisfilum usually relatively small.

Comments. This is the largest subgenus, containing 20 species, and is also the most difficult in which to identify the included species. It is often necessary to examine the male genitalia in order to make accurate determinations. Within geographical areas, the internal female genitalia are usually distinctive.

This subgenus can be divided into two groups based primarily on the structure of the spermatheca. In *T. boliviensis,* n. sp., *T. brasiliensis* Jensen-Haarup, *T. emarginata,* n. sp., and *T. hamulata,* n. sp., the sclerotized rod is somewhat elongate and lacks any subapical swelling. The remaining species have the sclerotized rod shorter and distinctly swollen subapically, becoming narrowed apically.

Thyanta (*Argosoma*) *testacea* (Dallas)
Figs. 169–183, Map 2

Pentatoma testacea Dallas, 1851:250; Walker, 1867:289.
Thyanta testacea: Stål, 1872:35; Berg, 1878:23, Lethierry and Severin, 1893:148; Kirkaldy, 1909:95.
Thyanta casta (of authors, not Stål): Uhler, 1893:705; Uhler, 1894b:174.
Thyanta signoreti Ruckes, 1956:65–66, fig. 7. NEW SYNONYMY.

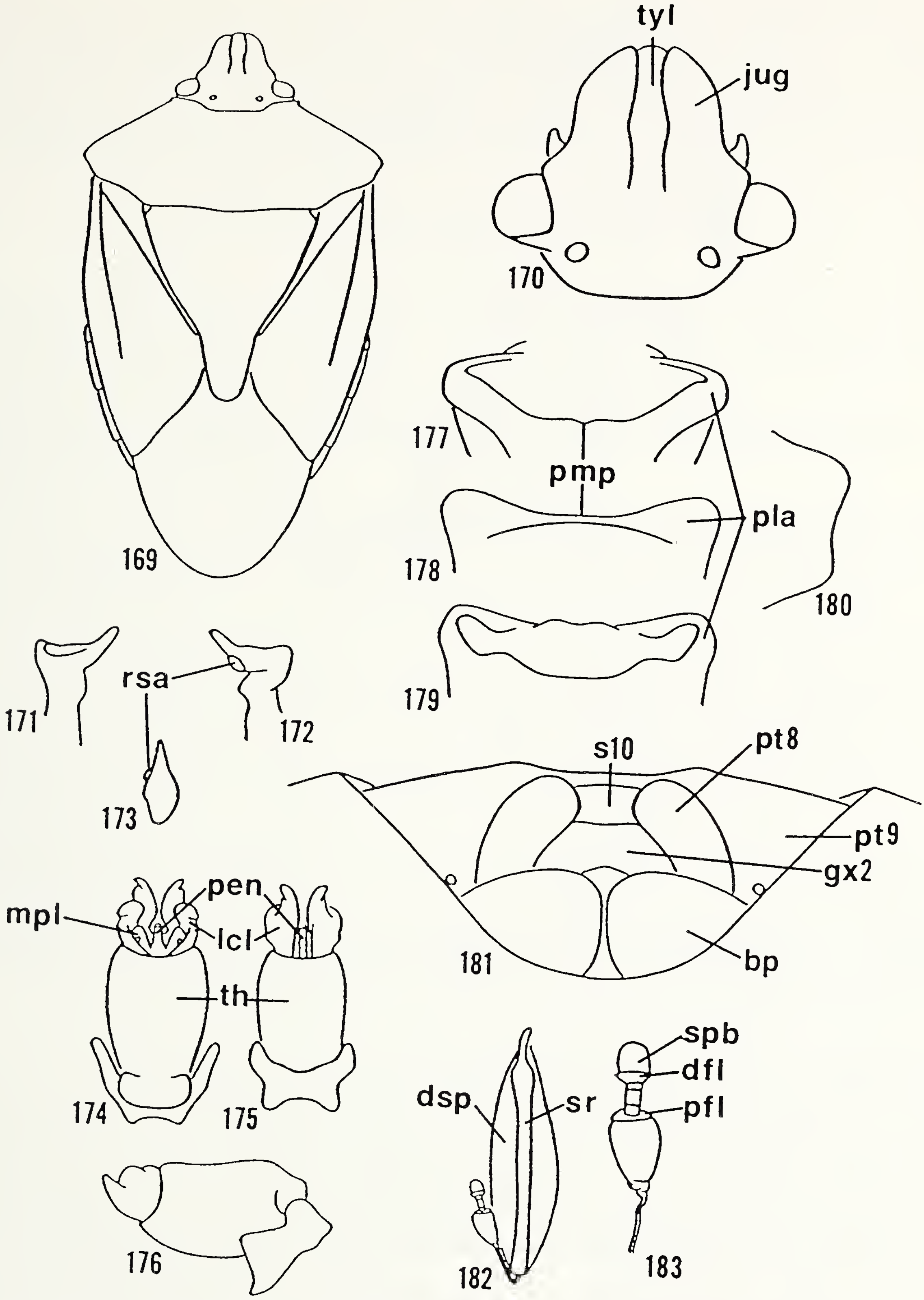
Diagnosis. General color green to brown, rarely with rubiginous transhumeral markings.

Outer jugal margins subparallel for middle third of distance from eyes to apex (Fig. 170). Anterolateral pronotal margins straight to slightly concave; humeral angles rounded to angulate, usually produced beyond base of adjacent coria by about one-half width of eye (Fig. 169). Pronotal cicatrices immaculate. Ostiolar canals acuminate apically. Posterolateral abdominal angles not marked with black or only minutely so; postspiracular black spots absent (sometimes evident in brown form).

Basal plates in caudoventral view with mesial margins convex, separated basally; posterior margins convex (Fig. 181). Distal end of sclerotized rod slightly swollen subapically, narrowed apically (Fig. 182); spermathecal duct greatly swollen below proximal flange, carrot-shaped (Fig. 183). Posterior margin of pygophore broadly and shallowly U-shaped in caudal view (Fig. 177); slightly concave in lateral view (Fig. 180). Each paramere apically acute in both medial and ectal views (Figs. 171, 173); concave surface oriented more dorsad than mediad; roughened spiculate area on lateral surface circular (Fig. 172). Aedeagus with dorsomedial lobe apparently absent (Fig. 175).

Types. Dallas (1851) described *Pentatoma testacea* from "S. America" without designating a holotype or paratypes, and it is not possible to determine how many syntypes he had. Only 1♀ syntype was located and is here designated lectotype. It has the following label data: (a) "Type" (b) "40 3.30 809" [ventral surface] (c) "36. PENTATOMA TESTACEA," [dorsal surface], "hil. 136, pl. 1, f. 5. Sign." [ventral surface]. The lectotype, which is conserved in the British Museum of Natural History (London), was examined.

Ruckes (1956) described *T. signoreti* from 1♂ and 3♀♀ from Colombia. The holotype and two paratypes were examined and do not differ in any significant way from *T. testacea.* The holotype is conserved in the Naturhistorisches Museum (Vienna, Austria).



Figs. 169–183. *T. testacea.* 169. Habitus. 170. Head. 171–173. Right paramere. 171. Medial view. 172. Lateral view. 173. Ectal view. 174–176. Theca and related structures. 174. Ventral view. 175. Dorsal view. 176. Lateral view. 177–180. Pygophore. 177. Caudal view. 178. Ventral view. 179. Dorsal view. 180. Lateral view. 181. Genital plates, caudoventral view. 182. Spermatheca. 183. Spermathecal pump. Symbols: bp, basal plate; dfl, distal flange; dsp, dilation of spermatheca; gx2, second gonacoxa; jug, juga; lcl, lateral conjunctival lobe; mpl, median penial lobe; pen, penisfilum; pfl, proximal flange; pla, posterolateral angle of pygophore; pmp, posterior margin of pygophore; pt8, eighth paratergite; pt9, ninth paratergite; rsa, roughened spiculate area on lateral surface of paramere; spb, spermathecal bulb; sr, sclerotized rod; s10, tenth sternite; th, theca; tyl, tylus.

Map. 2. *T.* (*A.*) *acuminata,* (○); *T.* (*A.*) *infuscata,* (▲); *T.* (*A.*) *patruelis,* (●); *T.* (*A.*) *sinuata,* (△); *T.* (*A.*) *straminea,* (*); *T.* (*A.*) *testacea,* (■); *T.* (*A.*) *xerotica,* (□).

Distribution. Lesser Antilles and northern South America (Map 2).

Specimens examined. 113 specimens collected during every month of the year; deposited in: AMNH, BMNH, CU, EGER, INHS, LACM, LHR, TAMU, USNM. COLOMBIA: *Cundinamarca:* Guayabetal; Melgar. *Magdalena:* La Jagua, 80 km S Valledupar; Pueblo Bello, 45 km W Valledupar, Sierra Nevada de S. Marta; Santa Marta. *Tolima:* Honda. VENEZUELA: Mesa de Playa. *Amazonas:* Gualtibo; Puerto Ayacucho. *Apure:* San Fernando. *Aragua:* 5 km NW Colonia Tovar; El Limón; Maracay; Rancho Grande. *Bolívar:* km 107 El Dorado Santa Elena. *Carabobo:* Mariara; Naguanagua. *Distrito Federal:* Serranía El Avila. *Guárico:* Calabozo; Hato El Samon cr. El Punzon Las Mercedes; Hato Las Lajas. *Lara:* 12 km N Cubiro; Torrellero. *Mérida:* 5 km NW Timotes. *Miranda:* El Jarillo Agua Fría. *Monagas:* Caripito; Jusepín; Maturín; 42 km SE Maturín. *Nueva Esparta:* El Robledar; Las Marites; Salamanca. *Portuguesa:* Aparición. *Sucre:* Cumaná. *Trujillo:* Cd de las Mesa de Esnujaque; Puerta. SURINAM: Mairmost Plantation. *Para:* Zanderij I., Boven.

Comments. Thyanta testacea can be reliably identified only by an examination of the male genitalia. The apically spinose parameres curving gently dorsad will separate

it from all other congeners except *T. patruelis.* The chin-like protuberance on the posteroventral surface of the pygophore is somewhat less prominent in *T. testacea* than in *T. patruelis.* There does seem to be a geographical separation of the two species with *T. testacea* restricted to northern South America and the Lesser Antilles and *T. patruelis* occurring from northeastern Brazil and southern Peru southward.

Thyanta (*Argosoma*) *patruelis* (Stål)
Figs. 184–198, Map 2

Pentatoma patruelis Stål, 1859:226–227; Walker, 1867:289.
Thyanta patruelis: Stål, 1862a:58; Stål, 1872:35; Berg, 1878:23; Lethierry and Severin, 1893:148; Kirkaldy, 1909:95.
Thyanta humilis Bergroth, 1891:225–226. NEW SYNONYMY.
Thyanta nitidula Ruckes, 1956:62–63, fig. 4; Rolston and McDonald, 1984:fig. 30. NEW SYNONYMY.

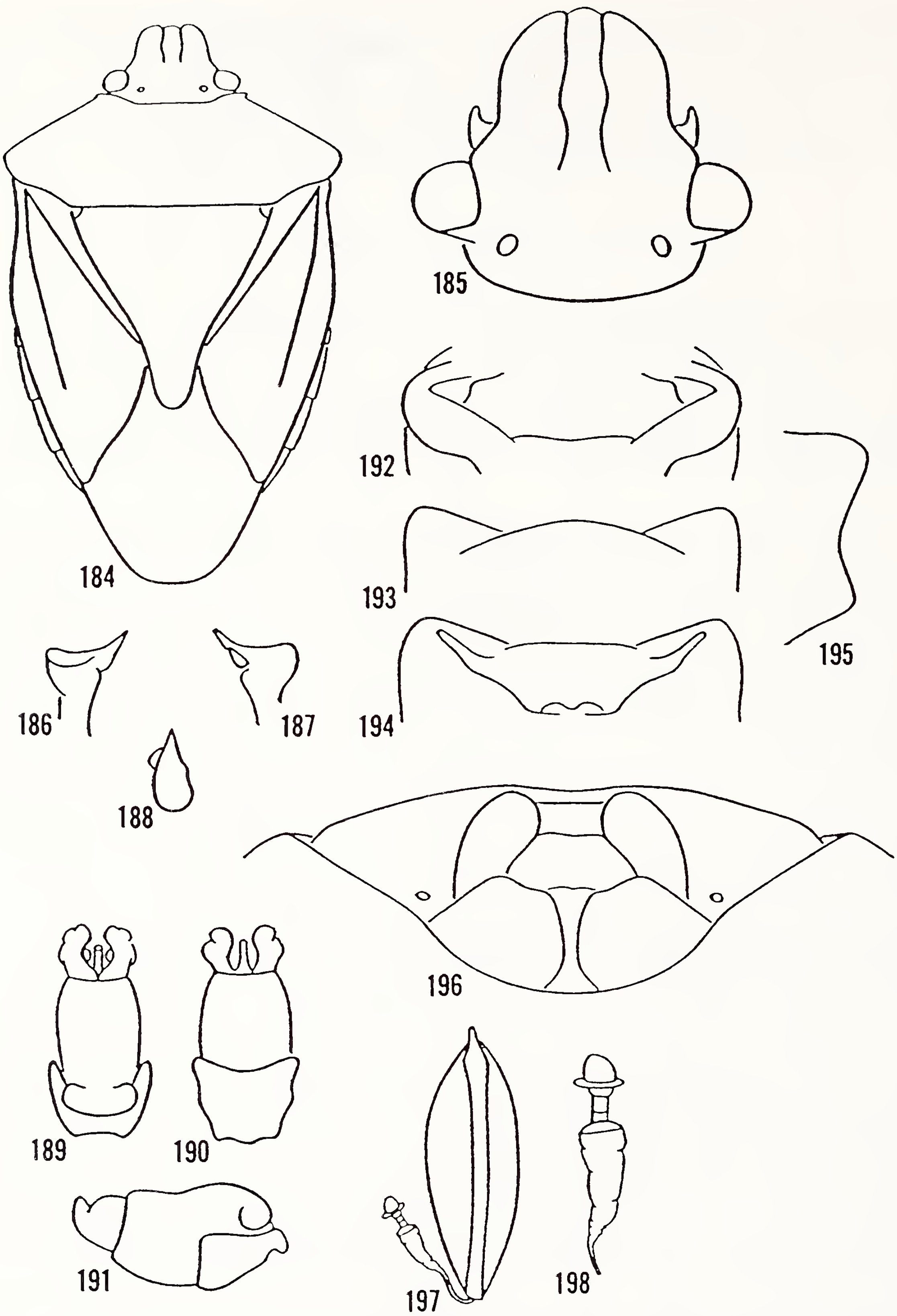
Diagnosis. Small to medium; dorsal surface green to brown, often with reddish-purple markings between humeral angles, on dorsal surface of head, on apex of scutellum, and on apex of each corium; punctures concolorous with surface.

Outer jugal margins subparallel for middle third of distance from eyes to apex (Fig. 185). Anterolateral margins of pronotum straight to weakly concave in dorsal view; humeral angles rounded to angulate, produced beyond base of adjacent coria by width of eye or less (Fig. 184). Pronotal cicatrices immaculate. Connexiva narrowly exposed; posterolateral angle of each segment usually marked with piceous, sometimes only minutely so. Ostiolar canals acuminate apically. Postspiracular spots lacking; posterolateral angles of abdominal sternites usually piceous.

Mesial margins of basal plates straight to slightly convex, separated basally; posterior margins straight to slightly convex; posteromesial angles rounded or slightly emarginate (Fig. 196). Sclerotized rod slightly swollen subapically, narrowed apically (Fig. 197). Spermathecal duct greatly swollen below proximal flange, carrot-shaped (Fig. 198). Posterolateral angles of pygophore only slightly prominent in lateral view (Fig. 195); posteroventral surface of pygophore distinctly depressed between blunt chin-like protuberance and posterior margin of pygophore; posterior margin of pygophore broadly and shallowly U-shaped in caudal view (Fig. 192). Apex of each paramere distinctly spinose in both medial and ectal views (Figs. 186, 188), roughened spiculate area on lateral surface ovoid (Fig. 187). Each lateral conjunctival lobe of aedeagus with 1–2 nonsclerotized diverticula (Fig. 191); dorsomedial lobe absent (Fig. 190); penisfilum small, median penial lobes spatulate, nearly hidden by conjunctival lobes (Fig. 189).

Types. Stål (1859) described *P. patruelis* from 1♀ specimen from Rio de Janeiro, Brazil. The holotype, which is conserved in the Naturhistoriska Rikoriska Rikomuseet (Stockholm, Sweden), was examined.

Bergroth (1891) described *Thyanta humilis* from at least two specimens from Minas Gerais, Brazil. Grazia (1987) made lectotype and paralectotype designations. The lectotype was examined, and is currently housed in the Museum National d'Histoire Naturelle (Paris, France). Although this specimen is smaller and somewhat more depressed than the holotype of *T. patruelis,* there are very few differences that will separate the two (see Comments below).



Figs. 184–198. *T. patruelis*. 184. Habitus. 185. Head. 186–188. Right paramere. 186. Medial view. 187. Lateral view. 188. Ectal view. 189–191. Theca and related structures. 189. Ventral view. 190. Dorsal view. 191. Lateral view. 192–195. Pygophore. 192. Caudal view. 193. Ventral view. 194. Dorsal view. 195. Lateral view. 196. Genital plates, caudoventral view. 197. Spermatheca. 198. Spermathecal pump.

Thyanta nitidula was described by Ruckes (1956) from 12♂♂ and 3♀♀, all from Brazil. The holotype was examined, and is conserved in the American Museum of Natural History (New York). This specimen is intermediate in size between the lectotype of *T. humilis* and the holotype of *P. patruelis* and falls within the range of variation exhibited by these two specimens (see Comments below).

Distribution. Central Brazil and southern Peru south to Argentina (Map 2).

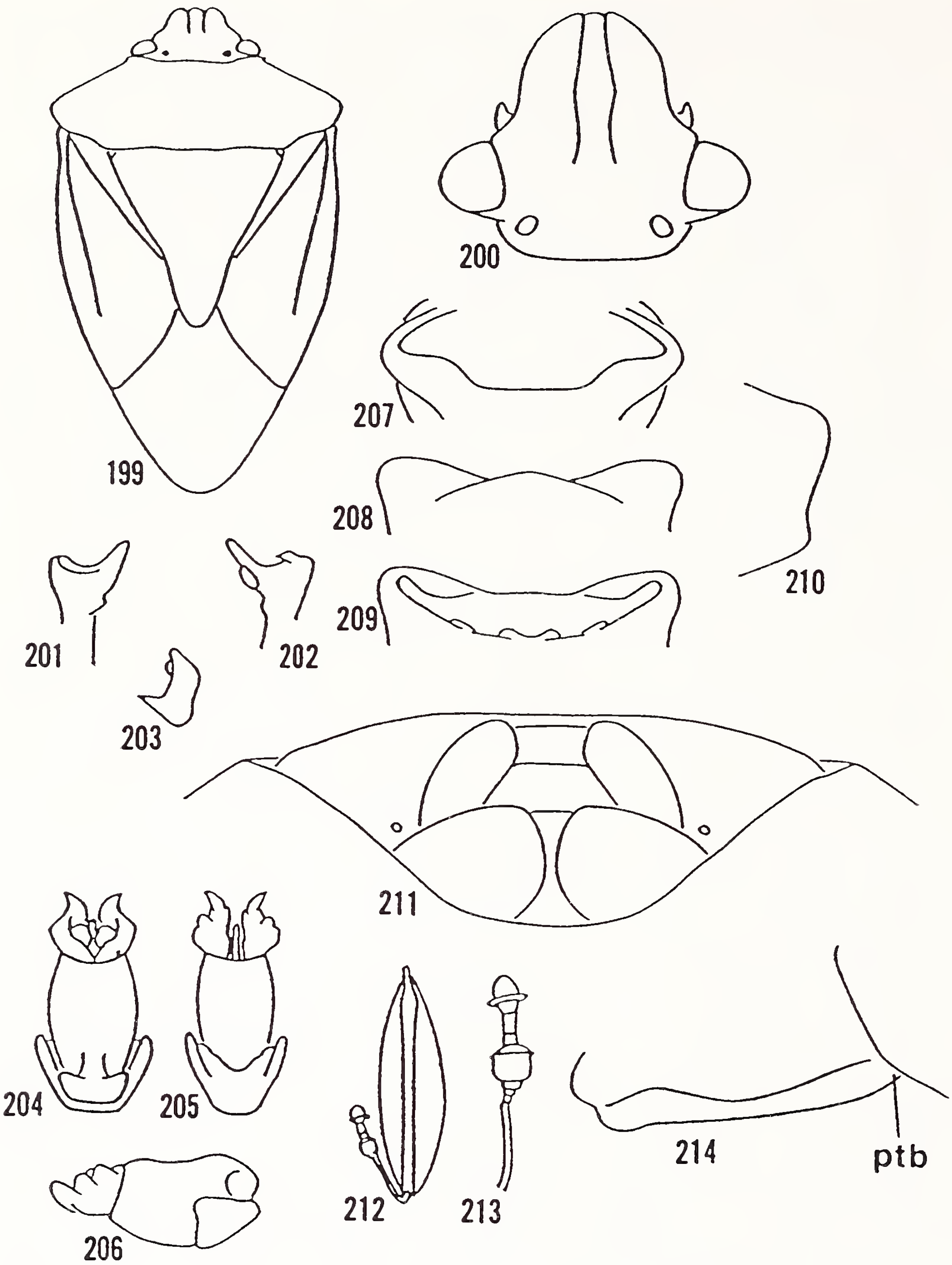
Specimens examined. 584 specimens collected during every month of the year except August; deposited in: AMNH, BMNH, CAS, CU, DAR, DBT, EGER, ISU, LACM, LHR, MBR, MGA, MCN, MNRJ, MZRS, OSU, POLH, PUL, SMEK, UEC, UMA, UNAM, USNM, ZMB. PERU: Curabaya; La Merced, Chanchamaya; *Cusco:* Quillabamba. *Junín:* 40–55 km SE Satipo. BRAZIL: Chapada de Guimaraes; Demerary; Lagoa de Camarim; Nordeste; Piriapolis. *Bahia:* Encruzilhada; Itap; Nova Conquista; Salvador. *Ceará:* Barbalha; Fortaleza. *Espírito Santo:* Guarapari; Linhares; Vitória. *Goiás:* Argarças; Brasília; Jataí. *Mato Grosso:* Cuiabá; Independencia. *Mato Grosso do Sul:* Aquidauna; Bodoqueña; Corumbá; Morro do Urucún; Rondonopolis. *Minas Gerais:* Carmo do R. Clavo; Cordisburgo; Pedra Azul; Bandeiro; Santa Barbara, Varginha. *Paraiba:* Juazeirinho. *Parañá:* Araucaria; 30 mi W Irati; Rolandia; Vila Velha Pk. *Pernambuco:* Bonito Prov.; Caruaru; Petrolina. *Rio de Janeiro:* Mangaratiba; Nova Iguaçu; Petrópolis; Quinta Boa Vista, Horto Botanica; Rio de Janeiro; Teresópolis. *Rio Grande do Sul:* Campos; Glorinha; Ipanema; Pelotas; Pôrto Alegre; Santa Maria; Taimbezinho, Parque Nacional dos Aparados da Serra Est.; Viamão; Vila Oliva. *Santa Catarina:* Corupá; Florianopólis; Nova Teutônia. *São Paulo:* 10 mi S Guapara; Piracicaba; São Paulo; São Vicenti. BOLIVIA: *Cochabamba:* Christal-Mayu, Prov. Chapare. *La Paz:* Yungas de La Paz. *Santa Cruz:* Buena Vista, Prov. Ichilo; Roboré; Saavédra-Malezas, Est. Expt. Agr.; Santa Cruz. PARAGUAY: *Asunción:* Asunción. Gran Chaco. *Central:* Areguá; Luque. *Chaco:* Río Negro. *Corrientes:* San Bernardino. *Guaira:* Villarrica. *Paraguarí. Presidente Hayes:* 42 km NW Benjamín Aceval. ARGENTINA: *Buenos Aires:* Isla Martín García; Punta Lara; San Isidrio. *Chaco. Corrientes:* San Roque. *Entre Ríos:* Leigre; Liebig. *Formosa:* Gran Guardia. *Misiones:* Apartado; Bompland; Eldorado; Let; Loreto; Posados; Puerto Iguazu; San Ignacio. *Santa Fe:* Villa Ana. URUGUAY: *Canelones:* Atlantida. *Montevideo:* Montevideo. *Paysondú:* Constancia. *Río Negro.*

Comments. Thyanta patruelis is a highly variable species with regard to both size and coloration. It is possible that it represents a group of several very closely related, morphologically indistinguishable species. Two specimens from opposite ends of the spectrum in variability (color, size) appear to be distinct species, but when a series of specimens are examined, it is obvious that all manner of intermediates exist. Also, no matter what the size or color of the specimen, the male and female genitalia are constant, with only minor variations in an occasional specimen.

Thyanta (*Argosoma*) *acuminata* Ruckes
Figs. 199–214, Map 2

Thyanta acuminata Ruckes, 1956:63–65, fig. 5.

Diagnosis. Small to medium; dorsal surface green to brown, sometimes with reddish markings on dorsal surface of pronotum and head; punctures usually concolorous with surface.



Figs. 199–214. *T. acuminata.* 199. Habitus. 200. Head. 201–203. Right paramere. 201. Medial view. 202. Lateral view. 203. Ectal view. 204–206. Theca and related structures. 204. Ventral view. 205. Dorsal view. 206. Lateral view. 207–210. Pygophore. 207. Caudal view. 208. Ventral view. 209. Dorsal view. 210. Lateral view. 211. Genital plates, caudoventral view. 212. Spermatheca. 213. Spermathecal pump. 214. Buccula, lateral view. Symbol: ptb, posterior termination of buccula.

Apex of head evenly rounded; outer jugal margins subparallel for middle third of distance from eyes to apex (Fig. 200). Anterolateral margins of pronotum straight to slightly concave in dorsal view; humeral angles rounded, protruding only slightly beyond base of adjacent coria (Fig. 199); pronotal cicatrices immaculate. Hemelytral membranes hyaline, lacking brown distal flecks. Posterolateral angles of connexival segments usually immaculate, sometimes minutely marked with black. Ventral sur-

face green to brown; posterolateral angles of abdominal sternites immaculate; postspiracular black spots absent. Ostiolar rugae acuminate apically.

Mesial margins of basal plates in caudoventral view convex, separated basally and distally; posterior margins convex; posteromesial angles broadly rounded (Fig. 211). Sclerotized rod relatively short, swollen subapically, gradually narrowing apically (Fig. 212). Swelling of spermathecal duct below proximal flange shorter than spermathecal pump and narrowing rather abruptly (Fig. 213). Posterior margin of pygophore in caudal view broadly and shallowly U-shaped, medial portion nearly straight (Fig. 207); posterolateral angles of pygophore prominent in both ventral and dorsal views (Figs. 208, 209); pygophore sinuous in lateral view (Fig. 210). Apex of each paramere in medial view narrowly rounded to spinose, curving gently dorsad (Fig. 201); concave surface oriented more dorsad than mediad; roughened, spiculate area on lateral surface oval (Fig. 202); possessing a distinct spinose lateral lobe in ectal view (Fig. 203). Aedeagus relatively small; each lateral conjunctival lobe with spinose diverticulum apically; median penial lobes spatulate; penisfilum relatively small, short (Figs. 204–206).

Types. Ruckes (1956) described this species from 13♂♂ and 4♀♀, all from Argentina and Paraguay. The holotype, which is conserved in the American Museum of Natural History (New York), was examined.

Distribution. Southern South America (Map 2).

Specimens examined. 197 specimens collected during every month of the year except July and September; deposited in: AMNH, BMNH, CAS, CU, DAR, EGER, ENGL, FSCA, LHR, MRB, SMEK, IML, UCS, UNL, USNM, ZMB. BOLIVIA: Mataral, V. Grande; Villa Vicencio. *Chuquisaca:* Monteagudo. *La Paz:* Iquisivi. *Santa Cruz:* Buena Vista, Prov. Ichilo; Colpa pump stn., 9 m W Warnes; Ingenio La Belgica, 38 km N Santa Cruz; 10 mi W Portachuelo; Rio Grande pump stn., 35 m S Santa Cruz; Saavedra Res. Stn. *Tarija:* Ing. Bermejo; Villa Montes. BRAZIL: *Minas Gerais:* Carmo do R. Claro. PARAGUAY: *Central:* nr. Ñemby. *Chaco:* Copagro, trans. Chaco km 589; Expt. Stn Fern. Col. *Concepción:* Horqueta. *Guaira:* Villarrica. *Nueva Asunción:* Parq. Nac. Tte. Enciso. *Presidente Hayes:* 42 km NW Benjamín Aceval; Gran Chaco. ARGENTINA: Laguna de Malvinas. *Catamarca:* Andalgala; Belén; Frías. *Chaco:* Colonia Benitez; Fortana; Labo Montevideo; Resistencia; Roque Saenz Peña. *Córdoba:* Alta Garcia; Guanaco Muerto. *Formosa:* Clorinda; 40 km SW Clorinda; Gran Guardia; La Florencia Este; 5 km N Pirané; 14 km SE Pirané. *Jujuy:* Perico. *La Rioja:* La Rioja; Patquia. *Salta:* Guemes; J N Gonzales; Tartagal; Rosario de la Frontera; Urundel. *Santa Fe:* Carcaraña. *Santiago del Estero:* Chaco, Rio Salada. *Tucumán:* Cardinal; El Bachi; La Aguadita; 11 km E de Las Cejas; San Miguel de Tucumán; Siambón.

Comments. This species can be separated from most other congeners by the reduction of nearly all black markings and by the lack of brown flecks in the hemelytral membranes. The acute lateral lobe of the parameres is a character this species shares only with *T. hamulata.* In *T. hamulata* the apex of each paramere curves dorsad and caudad forming a distinct hook, while in *T. acuminata* the apex of each paramere curves gently dorsad but does not form a hook. Also, the lateral lobe of the paramere in *T. hamulata* is triangular, while in *T. acuminata* it is digitiform and spinose apically.

Female specimens of *T. acuminata* can be distinguished from the other 3 species

of this subgenus which occur in southern South America by examining the spermatheca. *Thyanta boliviensis* and *T. brasiliensis* both have the sclerotized rod not at all swollen subapically; both *T. acuminata* and *T. patruelis* have this structure swollen subapically, although somewhat less so in *T. acuminata.* The swelling of the spermathecal duct below the proximal flange is much more extensive in *T. patruelis,* the length of the swelling being equal to or longer than the spermathecal pump. Also this swelling usually narrows gradually, giving the whole swollen portion the appearance of an inverted cone. In *T. acuminata,* this swollen portion is much shorter and narrows rather abruptly.

Thyanta (Argosoma) hamulata Rider, new species
Figs. 215–229, Map 3

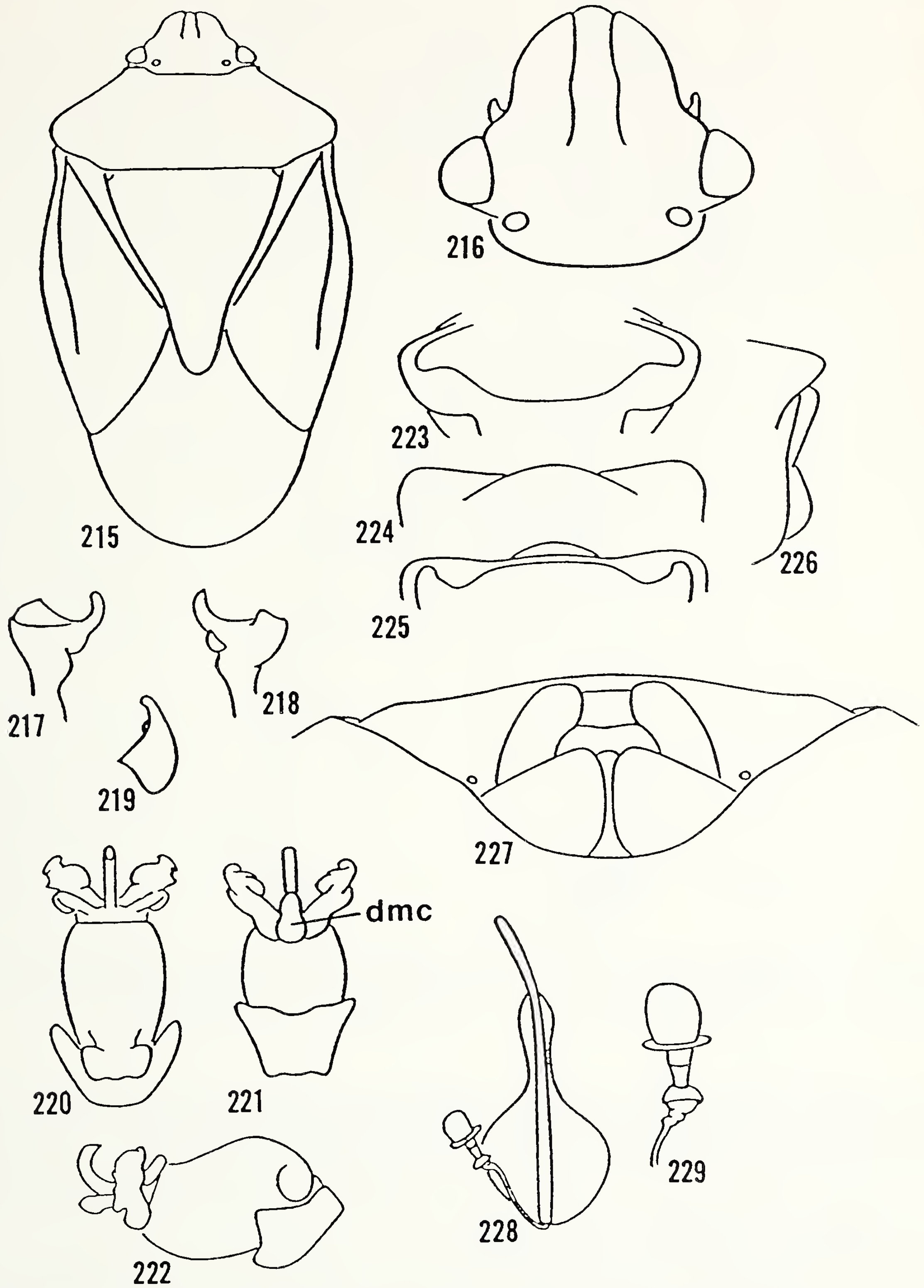
Description. Dorsal surface green to pale yellowish-brown, usually no red or black markings present; punctures concolorous with surface.

Apex of head broadly rounded; outer jugal margins sinuous (Fig. 216). Antennae pale brown to green, distal segments slightly darker. Anterolateral margins of pronotum in dorsal view nearly straight; humeral angles obtusely rounded, protruding slightly beyond base of adjacent coria (Fig. 215). Pronotal cicatrices immaculate. Hemelytra uniformly and shallowly punctate; posterior margins weakly convex; costal angles narrowly rounded (Fig. 215), reaching beyond middle of penultimate connexival segments; hemelytral membranes hyaline, a few faint brown flecks sometimes present. Connexiva narrowly or not at all exposed, posterolateral angles of segments sometimes minutely marked with piceous.

Ventral surface pale yellow to yellowish-green; punctures concolorous with surface; rostrum yellow to green, apical half of segment 4 piceous; reaching onto third (second visible) abdominal sternite. Ostiolar canals acuminate apically. Femora and tibiae yellowish-brown to green, tarsal segments sometimes darker. Postspiracular brown spots sometimes vaguely present in brown form; posterolateral angles of abdominal sternites usually immaculate, rarely marked minutely with black.

Mesial margins of basal plates in caudoventral view weakly convex, separated basally; posterior margins nearly straight; posteromesial angles rounded (Fig. 227). Sclerotized rod of nearly equal diameter throughout entire length, not at all swollen near apex; dilation of spermatheca constricted near middle, ending about three-fourths distance from base of sclerotized rod (Fig. 228); spermathecal duct only slightly swollen and coiled below proximal flange (Fig. 229). Posterior margin of pygophore in caudal view broadly and shallowly U-shaped, posterolateral angles somewhat thickened (Fig. 223); chin-like protuberance prominent in ventral and lateral views (Figs. 224, 226); posterior margin nearly straight in dorsal view (Fig. 225). Each paramere with concave surface oriented dorsad; in ectal view, apex narrowly rounded, digitiform, curving gently laterad, with angulate triangular lateral lobe (Fig. 219); from medial view apex curving dorsad and caudad forming a distinct hook (Fig. 217); roughed, spiculate areas on lateral surface of paramere localized, circular (Fig. 218). Each lateral conjunctival lobe of aedeagus with single diverticulum (Fig. 222); dorsomedial lobe present, but small (Fig. 221); penisfilum and median penial lobes of moderate size (Fig. 220).

Measurements. Total length 6.31–7.41 (6.39); total width 4.10–4.89 (4.10); medial length of pronotum 1.32–1.61 (1.32). Medial length of scutellum 2.80–3.31 (2.80);



Figs. 215–229. *T. hamulata.* 215. Habitus. 216. Head. 217–219. Right paramere. 217. Medial view. 218. Lateral view. 219. Ectal view. 220–222. Theca and related structures. 220. Ventral view. 221. Dorsal view. 222. Lateral view. 223–226. Pygophore. 223. Caudal view. 224. Ventral view. 225. Dorsal view. 226. Lateral view. 227. Genital plates, caudoventral view. 228. Spermatheca. 229. Spermathecal pump. Symbol: dmc, dorsomedial conjunctival lobe.

Map. 3. *T.* (*A.*) *boliviensis,* (○); *T.* (*A.*) *brasiliensis,* (●); *T.* (*A.*) *emarginata,* (*); *T.* (*A.*) *excavata,* (△); *T.* (*A.*) *hamulata,* (□); *T.* (*A.*) *obtusa,* (■); *T.* (*A.*) *vadosa,* (▲).

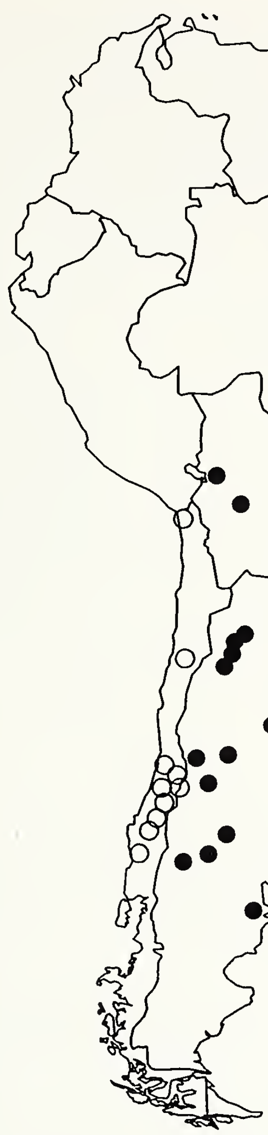
basal width 2.58–2.98 (2.58); width at distal end of frena 0.88–0.99 (0.92). Length of head 1.34–1.50 (1.37); width 1.88–2.08 (1.90). Length of segments 1–5 of antennae 0.37–0.42 (0.37), 0.74–0.98 (0.74), 0.81–0.98 (0.81), 0.99–1.21 (1.05), and 1.10–1.14 (1.10), respectively. Length of segments 2–4 of rostrum 1.18–1.29 (1.18), 0.75–0.81 (0.81), and 0.59–0.74 (0.59), respectively.

Holotype. ♂ labeled (a) "COLOMBIA: Dept. Valle del Cauca. Bitaco Valley, Finca Kyburz 1 km above Bitaco" (b) "Altitude 4500 ft. 27–28.XI.1963 P. C. Hutchinson & J. K. Wright." Deposited in the California Academy of Sciences (San Francisco).

Paratypes. 8♂♂, 9♀♀. Labeled same as holotype (2♂♂ 4♀♀ CAS); (a) "PERU:Dept. Cajamarca Prov. Jaén. Pucara. Rio Huancabamba, 900m 14–18.I.1964" (b) "P. C. Hutchison and J. K. Wright Collectors" (5♂♂ 2♀♀ CAS), except 2♂♂; labeled "10–13.I.1964"; "PERU: Dept. Amazonas Between Rio Marañón and Bagua. 3-X-1964 P. C. Hutchison & J. K. Wright" (♂ 2♀♀ CAS); and (a) "PERU: 94 mi. E. of Olmos, Lambayeque I-18-1955" (b) "E.I.Schlinger & E.S.Ross collectors" (♀ CAS).

Distribution. Northwestern South America (Map 3).

Comments. Only this species and *T. acuminata* have a distinct acute lateral lobe



Map. 4. *T.* (*P.*) *acuta,* (□); *T.* (*P.*) *acutangula,* (●); *T.* (*P.*) *cornuta,* (■); *T.* (*P.*) *fimbriata,* (▲); *T.* (*P.*) *juvenca,* (○); *T.* (*P.*) *robusta,* (△).

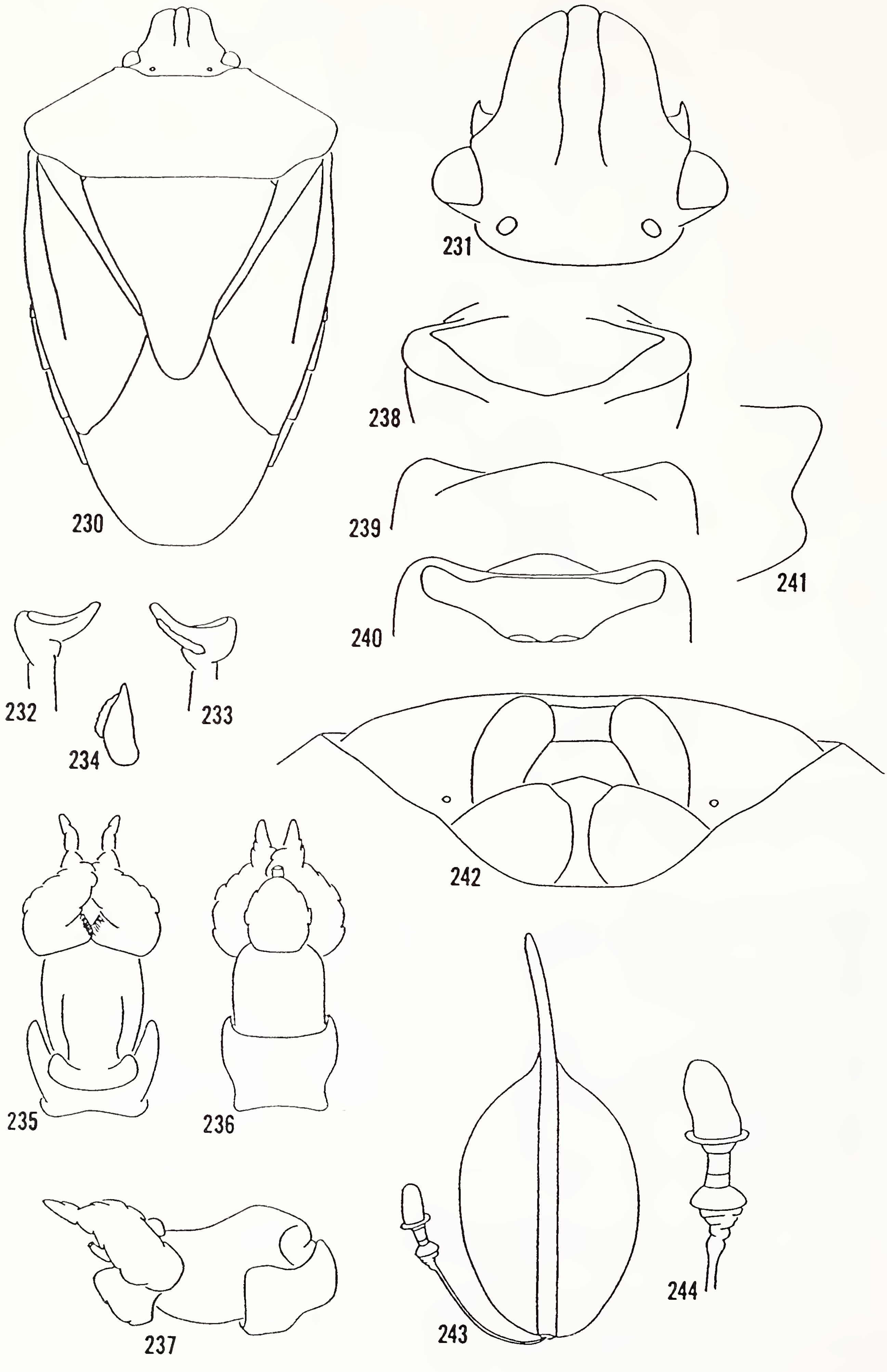
on each paramere. In *T. hamulata,* the lateral lobe is triangular, and the apex of each paramere curves dorsad and caudad, forming a distinct hook. In *T. acuminata,* the lateral lobe is spinose, and the apex of each paramere curves gently dorsad, not forming a distinct hook.

Only four species of *Thyanta* are known to lack the subapical swelling of the sclerotized rod of the spermatheca. *Thyanta emarginata* has the posteromesial angle of each basal plate deeply excavated. *Thyanta hamulata* can be separated from both *T. brasiliensis* and *T. boliviensis* by the constriction in the middle of the dilation of the spermatheca.

Etymology. Named for the hamulate or hooked apex of each paramere.

Thyanta (Argosoma) boliviensis Rider, new species
Figs. 230–244, Map 3

Description. Medium to large; dorsal surface olive green to reddish-brown; often with reddish-purple markings between humeral angles, on dorsal surface of head, and on apex of scutellum; punctures concolorous with surface.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Apex of head evenly rounded; outer jugal margins sinuous (Fig. 231). Punctures on head rather dense, surface sometimes appearing reticulate. Antennae green to pale brown, distal 3 segments usually marked with red. Anterolateral margins of pronotum straight in dorsal view; humeral angles rounded to nearly angulate, produced beyond base of adjacent coria by one-half width of eye or less (Fig. 230). Pronotal cicatrices immaculate. Hemelytral punctures shallow, slightly more dense on exocorium; posterior margins slightly convex; costal angles narrowly rounded, usually reaching to middle of penultimate connexival segments (Fig. 230); hemelytral membranes hyaline, usually lacking all brown flecks. Connexiva narrowly exposed, posterolateral angles of segments piceous.

Ventral surface yellowish-green to brown; punctures concolorous with surface. Rostrum pale brown, apical half of segment 4 piceous, reaching onto base of third (second visible) abdominal segment. Ostiolar canals acuminate apically. Femora and tibiae pale brown, tarsal segments and distal third of each tibia sometimes darker. Postspiracular spots lacking; posterolateral angles of abdominal sternites piceous.

Mesial margins of basal plates convex, separated basally and distally; posterior margins straight to slightly convex; posteromesial angles slightly emarginate (Fig. 242). Sclerotized rod elongate, neither swollen subapically nor abruptly narrowed apically; dilation of spermatheca extending about three-fourths length of sclerotized rod, not abruptly narrowed on apical fourth (Fig. 243); spermathecal bulb slightly elongate, spermathecal duct with small amount of coiling below proximal flange (Fig. 244). Posterior margin of pygophore sinuously U-shaped in caudal view, medial portion slightly concave (Fig. 238); pygophore emarginate in lateral view (Fig. 241); posterolateral angles not distinctly prominent in ventral or dorsal views (Figs. 239, 240). Apex of each paramere acute, nearly spinose in medial view (Fig. 232); paramere slightly lunate in ectal view, apex nearly spinose (Fig. 234); roughened, spiculate area on lateral surface of paramere linear in shape (Fig. 223), corresponding black carina on wall of pygophore also linear. Each lateral conjunctival lobe of aedeagus with one acute diverticulum apically and one obtuse slightly sclerotized diverticulum ventrally (Fig. 235); dorsomedial lobe well developed (Fig. 236); penisfilum and median penial lobes nearly hidden by conjunctiva (Fig. 237).

Measurements. Total length 7.41–9.90 (7.73); total width 4.73–6.07 (4.89); medial length of pronotum 1.40–1.82 (1.51). Medial length of scutellum 3.05–4.08 (3.13); basal width 3.02–3.86 (3.13); width at distal end of frena 0.99–1.32 (1.03). Length of head 1.57–1.82 (1.64); width 2.03–2.32 (2.12). Length of segments 1–5 of antennae 0.48–0.55 (0.52), 0.75–0.99 (0.81), 1.10–1.32 (1.25), 1.32–1.53 (1.47), and 1.36–1.44 (1.44), respectively. Length of segments 2–4 of rostrum 1.21–1.51 (1.21), 0.81–0.96 (0.85), and 0.81–0.99 (0.92), respectively.

Holotype. ♂ labeled (a) "Yungas de La Paz, Bolivia Dec. 4–20, 1955, 1200–1700

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Figs. 230–244. *T. boliviensis.* 230. Habitus. 231. Head. 232–234. Right paramere. 232. Medial view. 233. Lateral view. 234. Ectal view. 235–237. Theca and related structures. 235. Ventral view. 236. Dorsal view. 237. Lateral view. 238–241. Pygophore. 238. Caudal view. 239. Ventral view. 240. Dorsal view. 241. Lateral view. 242. Genital plates, caudoventral view. 243. Spermatheca. 244. Spermathecal pump.

M Luis E. Pena, Collector" (b) "J C Lutz Collection 1961." Deposited in the U.S. National Museum of Natural History (Washington, D.C.).

Paratypes. 44♂♂, 66♀♀. Labeled same as holotype (4♂♂ 2♀♀ USNM); labeled as holotype, except lacking (b) (6♂♂ 4♀♀ AMNH, FSCA); labeled as holotype, except (b) "Thyanta humeralis Ruckes Det. J. C. Lutz" (♂ AMNH); labeled as holotype, except (b) "Thyanta humeralis Ruckes Lutz '57" (♂ 2♀♀ AMNH, FSCA); "Coripata 1700m. Yungas La Paz Bol. 1-XII-1984 Coll. L.E.Pena" (6♀♀ USNM); "Pte. Mururata Yungas La Paz Bol. 1200–1600m. 24–26-XII-1984 Coll. L.E.Pena" (4♂♂ 5♀♀ USNM); "Chulumani Yungas La Paz Bol. XII-1984 Coll. L.E.Peña" (♀ USNM); (a) "BOLIVIA: Dpt. La Paz, Prov. Sud Yungas, 21 km. W. Chulumani. 4050'.27-V-1989. J.E. Eger, coll." (b) "J.E. Eger Collection" (2♂♂ 4♀♀ EGER); (a) "BOLIVIA: Dpt. La Paz, Prov. Sud Yungas, Puente Villa. 4300'.19–24-V-1989. J.E. Eger, coll." (b) "J.E. Eger Collection" (2♂♂ 5♀♀ EGER); "(SE) Coroico 1800–2100m. La Paz Bol. 30-XI–2-XII-84 Coll. L.E.Pena G." (♂ USNM); "Rio Coroico 1200m. La Paz Bol. 24–26-XI-84 Coll. L.E.Pena" (10♂♂ 6♀♀ USNM); (a) "Bolivia, Coroico 20.12.48 A. Martinez" (b) "C J Drake Coll. 1956" (♂ USNM); (a) "Coroico Bolivia" (b) "H G Barber Colln 1950" (♂ ♀ USNM); (a) "BOLIVIA, L.P., 1190 m.,1 mi,E.Puente Villa,S.Yungas IV-8-1978 C&L O'Brien" (b) "Thyanta misc ♀♀" (♀ ENGL); "Circuata-Cajuata 2400 m. La Paz Bol. 3–5-XII-84 Coll. L.E.Pena" (2♂♂ 2♀♀ USNM); "Monteagudo Chuquisaca Bol. 24-XII-84 Coll. L.E.Pena" (4♀♀ USNM); "(E) Muyupampa 1600 m. Chuquisaca Bol. 21–25-XII-84 Coll. L.E.Pena G." (2♂♂ 3♀♀ USNM); "Mataral (N) V. Grande Bol. 1800–2000m. 15–17-XII-1984 Coll. L.E.Pena" (♀ USNM); "Sta. Rosa 1100 m. (N) Mataral Bol. 15-XII-84 Coll. L.E.Pena" (3♂♂ 3♀♀ USNM); "Pto. Camacho (S) Sta. Cruz Bol. 20-XII-84 Coll. L.E.Pena" (♀ USNM); "Comarapa 1800 m. Santa Cruz Bol. 14-XII-84 Coll. L.E.Pena" (♀ USNM); "TRES ESTEROS Guanay, Boliv 19/25-Aug-89 leg: L.E. Peña" (♀ USNM); (a) "Rurrenabaque Beni Bolivia WMMMann" (b) "Nov. 1921" (c) "MULFORD BIOLOGICAL EXPLORATION 1921–1922" (♀ USNM); "Coripata" (♂ 5♀♀ MLP), except 1♀ with (b) "Thyanta, P. DENIER det." (MLP); (a) "Ost Bolivien Prov. Lara 750 m Steinbach S.V." (b) "Z.M.B. Hem." (♀ ZMB); "caranavi" (♀ MLP); "Corzuela n 8.1.36" (♀ MLP); "Peru, 2400m alt. Dept Cusco Machu Picchu VII,14–15,1951 sweeping G.H. Dieke" (♀ USNM); (a) "Macchu Picchu Ruins, Cuzco, Peru March 6 1947 Alt. 9500 ft." (b) "J. C. Pallister Coll. Donor Frank Johnson" (c) "Thyanta patruelis Stål det. H. Ruckes" (♀ AMNH); "PERU: Cuzco, Pisac, 3,000m. 15.viii.1971 C. & M. Vardy B.M. 1971-533" (♂ BMNH); (a) "Abancay, PERU. III-6-51" (b) "Ross and Michelbacher Collectors" (2♀♀ CAS); (a) "Arg. Salta Positos II.50 A. Martiñez" (b) "C J Drake Coll. 1956" (♂ USNM); and (a) "AcSA: 217C ARGENTINA TUCUMAN Cadillal s/Solanum auriculatum 15/11/85 ERG" (b) "Thyanta sp. Det. T. J. Henry 1987" (♂ USNM).

Distribution. Southeastern Peru, Bolivia, and northern Argentina (Map 3).

Comments. In general appearance this species resembles larger specimens of *T. patruelis,* but it is more closely related to *T. brasiliensis.* Male specimens can be separated from all other species in the subgenus *Agrosoma* by the elongate, linear spiculate area on the lateral surface of each paramere. Male and female specimens can usually be distinguished from *T. brasiliensis* by the less prominent humeral angles. The only way to reliably separate females of *T. boliviensis* and *T. patruelis* is by examining the spermatheca of each species. In *T. boliviensis,* the sclerotized rod is neither swollen subapically nor abruptly narrowed apically as it is in *T. patruelis.*

Only *T. brasiliensis, T. emarginata, T. excavata,* and *T. hamulata* have the sclerotized rod as described above. *Thyanta emarginata* can be identified by the distinctly excavated basal plates; the remaining three species can be distinguished by the condition of the dilation of the spermatheca. In *T. boliviensis* this structure is in the form of a single balloon-like structure; in *T. brasiliensis* it is abruptly narrowed for the distal half; and in *T. hamulata* it is constricted in the middle and then dilates again, forming a figure 8 shape.

Etymology. Named for the country of the type locality.

Thyanta (*Argosoma*) *brasiliensis* Jensen-Haarup
Figs. 245–259, Map 3

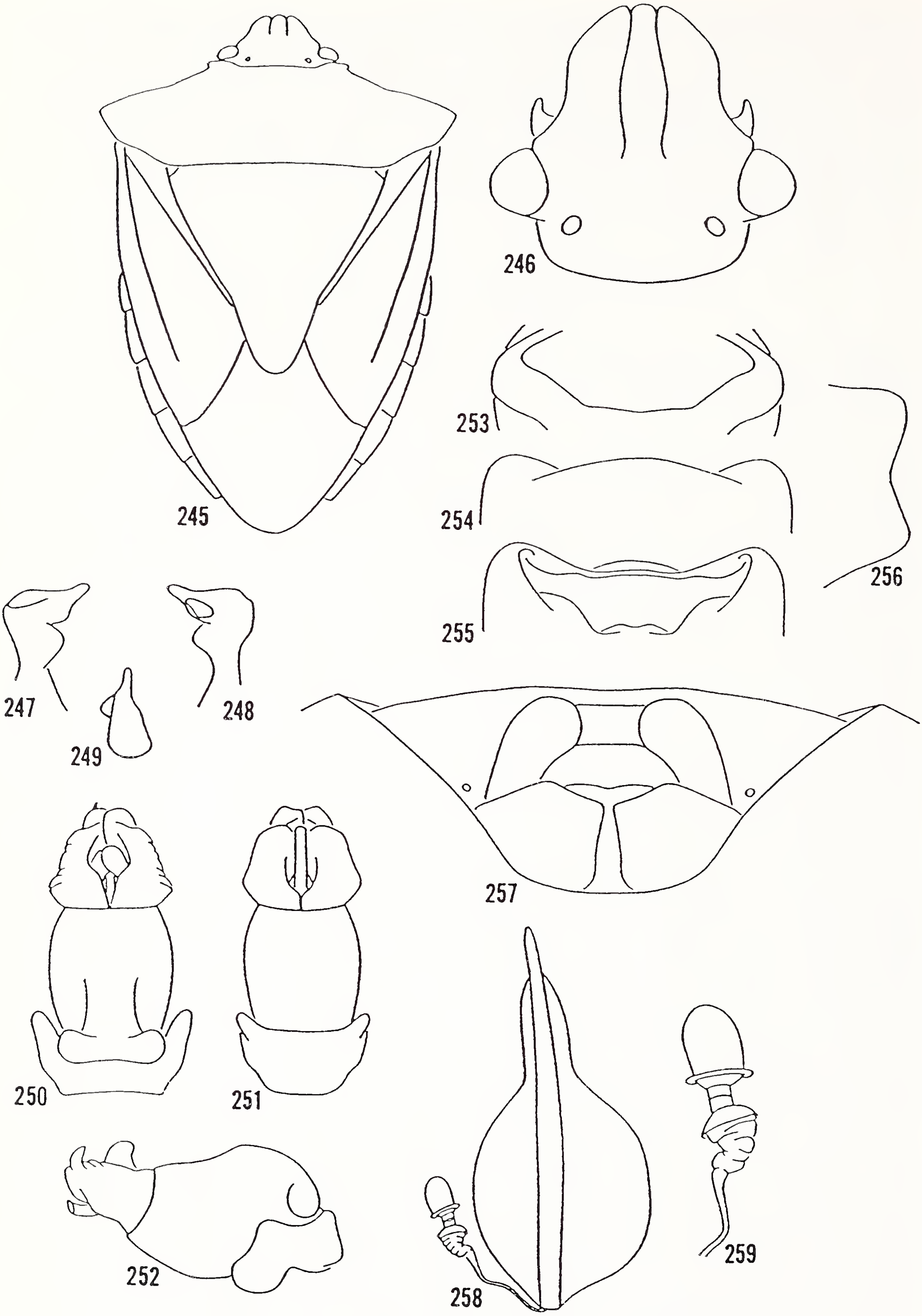
Thyanta brasiliensis Jensen-Haarup, 1928:187, 189–190.
Thyanta humeralis Ruckes, 1956:57–59, fig. 2. NEW SYNONYMY.

Diagnosis. Medium to large, robust; extremely variable in coloration. One form green to pale brown, usually with dark reddish-purple markings between humeral angles, on dorsal surface of head, and on apex of scutellum. Second form pale green to fuscous, sometimes tending to purplish, often with anterior two-thirds of pronotal disc much paler than rest, sometimes with numerous interstellate pale points on coria. Punctures usually concolorous with surface, sometimes brown.

Outer jugal margins nearly parallel for middle third of distance from eyes to apex (Fig. 246). Anterolateral margins of pronotum in dorsal view concave; humeral angles narrowly rounded to angulate, sometimes marked with black, extending beyond base of adjacent coria by one-half width of eye or more (Fig. 245); pronotal cicatrices not marked with black. Hemelytral membranes hyaline, often with a few brown flecks. Posterolateral angles of connexival segments usually piceous. Postspiracular black spots usually lacking, sometimes present in darker specimens; posterolateral angles of abdominal sternites piceous.

Mesial margins of basal plates in caudoventral view nearly straight, separated basally; posterior margins sinuously convex; posteromesial angles narrowly rounded (Fig. 257). Sclerotized rod not at all swollen subapically, gradually tapering to a narrowly rounded apex; dilation of spermatheca single, but abruptly narrowed for distal third, ending a short distance from apex of sclerotized rod (Fig. 258); spermathecal duct with a moderate amount of coiling below proximal flange (Fig. 259). Posterior margin of pygophore in caudal view broadly U-shaped, medial portion nearly straight (Fig. 253); lateral angles of pygophore and blunt chin-like protuberance prominent when viewed laterally (Fig. 256). Apex of each paramere narrowly rounded, nearly spinose in ectal view (Fig. 249); concave surface oriented more mediad than dorsad, apex narrowly rounded in medial view, shaft with prominent protuberance just below parameral head (Fig. 247); roughened, spiculate area on lateral surface obovate (Fig. 248). Each lateral conjunctival lobe of aedeagus with one acute diverticulum (Fig. 252); median penial lobes relatively large (Fig. 250); penisfilum medium in size; dorsomedial conjunctival lobe apparently absent (Fig. 251).

Types. Jensen-Haarup (1928) described *T. brasiliensis* from 1♂ and 1♀ without designating a holotype. The ♂ labeled (a) "♂" (b) "Type Coll. J=Hrp." (c) "Type" (d) "Thyanta brasiliensis J-Hrp Coll. Jensen Haarup." (e) "Lagoa Santa Reinhardt" is designated lectotype. The ♀ labeled (a) "♀" (b) "Type Coll. J=Hrp." (c) "Type" (d)



Figs. 245–259. *T. brasiliensis.* 245. Habitus. 246. Head. 247–249. Right paramere. 247. Medial view. 248. Lateral view. 249. Ectal view. 250–252. Theca and related structures. 250. Ventral view. 251. Dorsal view. 252. Lateral view. 253–256. Pygophore. 253. Caudal view.

"Rio de Janeiro Reinhardt" (e) "Thyanta brasiliensis Jensen-Haarup leg." is designated paralectotype. Both specimens were examined and are housed in the Universitets Zoologiske Museum (Copenhagen, Denmark).

Ruckes (1956) described *T. humeralis* from 9♂♂ and 10♀♀. The holotype was examined, although it is slightly larger than the type of *T. brasiliensis,* there is no other significant difference. The holotype of *T. humeralis* is located in the American Museum of Natural History (New York).

Distribution. Southern South America (Map 3).

Specimens examined. 163 specimens collected during every month of the year; deposited in AMNH, BMNH, CAS, CU, DAR, DBT, EGER, FSCA, IML, LHR, MCN, MGA, OSU, UEC, USNM, ZMB, ZMUC. PERU: *Junín:* Satipo. *Loreto:* Guyabamba, near Iquitos. BRAZIL: Lagoa Santa; Rodcio. *Esperíto Santo:* Vitória. *Mato Grosso:* Cuiabá. *Mato Grosso do Sul:* Corumbá; Miranda. *Minas Gerais:* Varginha. *Pará:* Jacaréacanga. *Parañá:* 5 mi E Maravilha. *Rio de Janeiro:* Rio de Janeiro; Teresópolis. *Rio Grande do Sul:* Pôrto Alegre. *Santa Catarina:* Anita Garibaldi Est.; Nova Teutônia. *São Paulo:* Bebedouro; Campinas; Cosmopolis; Indiana; Piracicaba. BOLIVIA: Villa Vicencia. *Cochabamba:* Chapare, Christal-Mayu. *El Beni:* Trinidad. *La Paz:* Coroico; Rurrenabaque. *Santa Cruz:* Buena Vista; Montero; Saavedra. PARAGUAY: San Luis. *Alto Parañá:* Puerto Presidente Stroessner. *Caaguazú:* Estancia Primera. *Central:* Nueva Italia. *Concepción:* Horqueta. *Cordillera:* Inst. Agro. Nac., Caacupé; San Bernardino; 20 km NW San Bernardino. *Guaira:* Villarica. *Itapúa:* Trinidad. *Paraguarí:* Sapucaí. *Presidente Hayes:* Gran Chaco. ARGENTINA: *Córdoba:* Sierra de Córdoba, Cosquin. *Misiones:* Apartado; Eldorado; Leandro Alem; Let; Puerto Iguazú; Puerto Rico; Victoria.

Comments. This species occurs in two fairly distinct color forms, but an examination of the genitalia of both sexes and other morphological characters reveals no significant differences. Because some specimens intermediate between the two forms do occur, it is believed that all specimens belong to a single variable species.

This species can be recognized from other congeners by the robust shape, sometimes by the dorsal coloration, often by the distinctly prominent humeral angles and the posteroventral production of the pygophore when viewed laterally, and by the shape of the parameres. Females can be identified by the shape of the spermatheca. It is the only species with the sclerotized rod not swollen subapically and with a single dilation of the spermatheca that is abruptly narrowed distally for a short distance.

Thyanta (Argosoma) emarginata Rider, new species
Figs. 260–264, Map 3

Description. Dorsal surface olive-brown, head and anterior two-thirds of pronotum slightly darker; apex of scutellum reddish; punctures reddish-brown.

Apex of head evenly rounded; outer jugal margins sinuous, nearly parallel for middle third of distance from eyes to apex (Fig. 261); surface of head rather densely punctate, juga appearing somewhat reticulate. Antennae pale brown, some reddish

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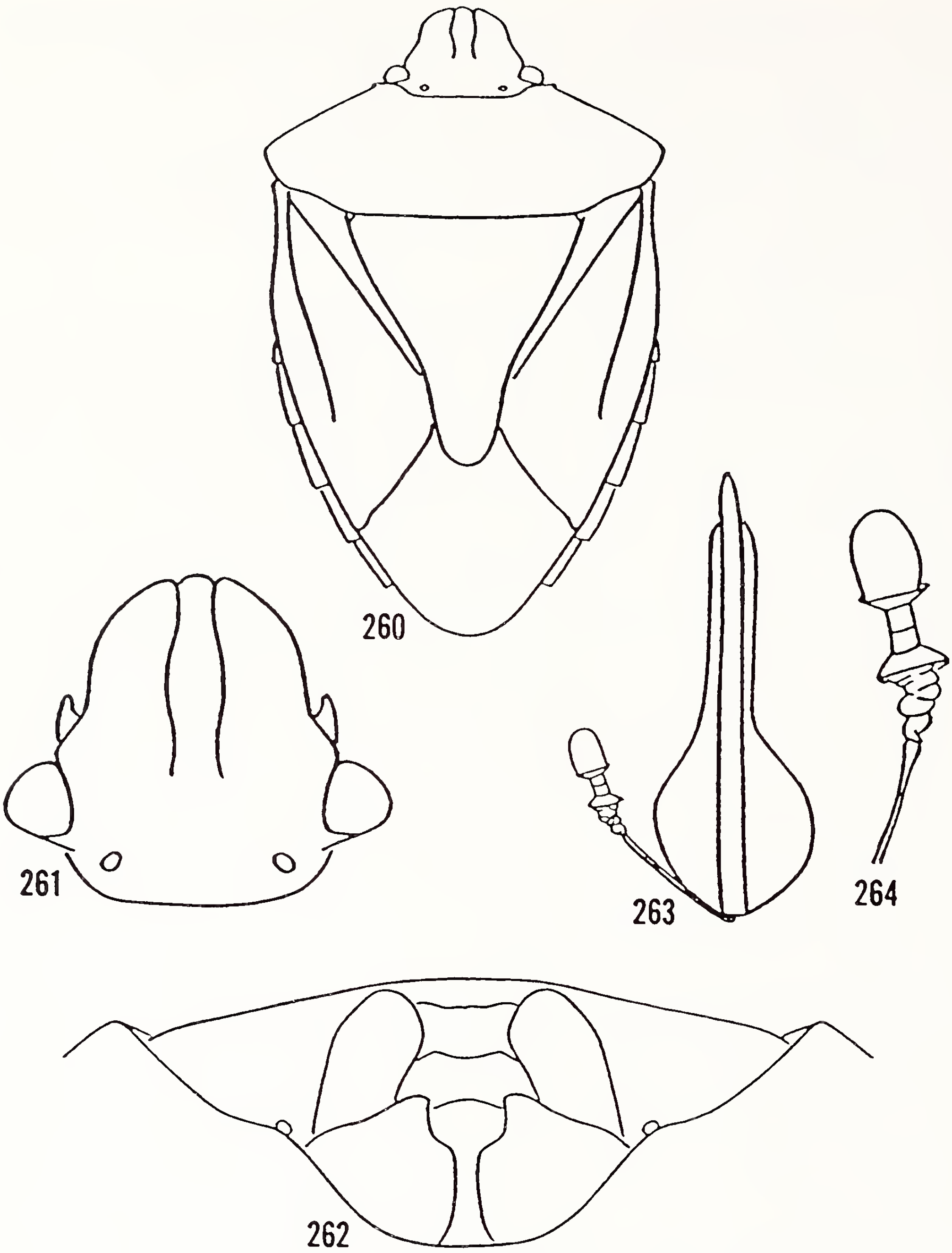
254. Ventral view. 255. Dorsal view. 256. Lateral view. 257. Genital plates, caudoventral view. 258. Spermatheca. 259. Spermathecal pump.



Figs. 260–264. *T. emarginata.* 260. Habitus. 261. Head. 262. Genital plates, caudoventral view. 263. Spermatheca. 264. Spermathecal pump.

hues on distal 3 segments. Anterolateral margins of pronotum straight in dorsal view; humeral angles rounded, nearly angulate, apex piceous, protruding slightly beyond base of adjacent coria (Fig. 260). Surface of pronotum transversely depressed just posterior to pronotal cicatrices; each pronotal cicatrice marked with fuscous in mesial angle. Hemelytra rather uniformly punctate; posterior margins weakly convex; costal angles reaching beyond middle of penultimate connexival segments (Fig. 260); hemelytral membranes hyaline. Connexiva narrowly exposed, stramineous; posterolateral angles of segments piceous.

Ventral surface pale yellowish brown; punctures concolorous. Rostrum stramineous, segment four black on apical half, reaching to near posterior margin of third (second visible) abdominal sternite. Ostiolar canals acuminate apically. Femora and

tibiae stramineous to pale brown. Postspiracular black spots absent; posterolateral angles of abdominal sternites piceous.

Mesial margins of basal plates in caudoventral view slightly convex; posterior margins sinuous; posteromesial angles deeply excavated; concavity resulting from excavations in basal plates nearly as long as wide, with lateral sides nearly parallel (Fig. 262); surface of basal plates distinctly rugose, area near excavation fuscous. Sclerotized rod relatively elongate, not at all swollen subapically; dilation of spermatheca single, but abruptly narrowed for distal two-thirds of length of sclerotized rod (Fig. 263); spermathecal duct moderately swollen and coiled below proximal flange (Fig. 264). Male unknown.

Measurements. Total length 8.36; total width 5.41; medial length of pronotum 1.73. Medial length of scutellum 3.50; basal width 3.20; width at distal end of frena 1.21. Length of head 1.70; width 2.12. Length of segments 1–5 of antennae 0.49, 0.83, 0.99, 1.18, and 1.25, respectively. Length of segments 2–4 of rostrum 1.32, 0.88, and 0.87, respectively.

Holotype. ♀ labeled "Peru. Dpto. La Libertad Cumpang. above Uctubamba. 2625 M. 13 X 1979. L. J. Barkley." Deposited in the U.S. National Museum of Natural History (Washington, D.C.). No paratypes.

Distribution. Peru (Map 3).

Comments. Although several species of *Thyanta* are known to have the posteromesial angle of the basal plates weakly emarginate, only three have this angle deeply emarginate. The resulting concavity in the basal plates of *T. vadosa* is much more shallow and the sides are divergent; both *T. emarginata* and *T. excavata* have the concavity deeper, with the sides nearly parallel. *Thyanta emarginata* differs from *T. excavata* by having the resulting concavity nearly as long as wide, and by the distinctly rugose surfaces of the basal plates, which are weakly rugose in *T. excavata.*

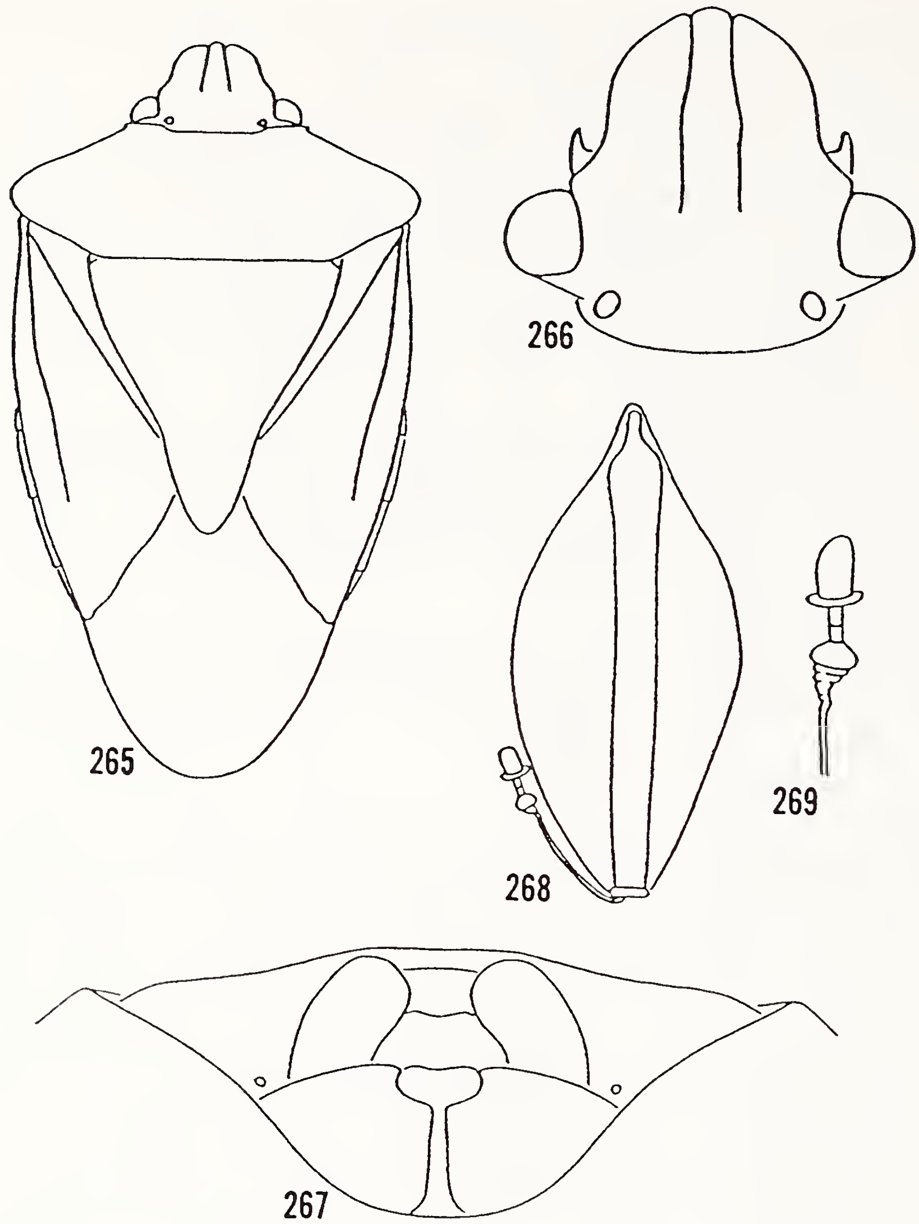
Thyanta emarginata further differs from both *T. vadosa* and *T. excavata* by the structure of the spermatheca. The sclerotized rod in *T. emarginata* is not swollen subapically as it is in *T. vadosa* and *T. excavata.* The nonswollen sclerotized rod is a character that *T. emarginata* shares only with *T. hamulata, T. brasiliensis,* and *T. boliviensis.* None of these three species have the basal plates excavated.

Etymology. Named for the distinctly emarginate posteromesial angles of the basal plates.

Thyanta (Argosoma) excavata Rider, new species
Figs. 265–269, Map 3

Description. Dorsal surface glossy, pale to medium green with reddish-purple transhumeral band, sometimes with reddish-purple coloration on dorsal surface of head, on apex of scutellum, and on apex of coria; punctures concolorous with surface.

Apex of head evenly rounded, outer jugal margins subparallel for middle third of distance from eyes to apex (Fig. 266). Antennae pale reddish-green, distal two segments slightly darker. Anterolateral margins of pronotum in dorsal view nearly straight; humeral angles obtusely rounded, protruding only slightly beyond margin of adjacent coria (Fig. 265). Pronotal cicatrices immaculate. Hemelytra uniformly and shallowly punctate; posterior margins nearly straight; costal angles narrowly rounded to angulate, extending to beyond middle of penultimate connexival segments; hemelytral



Figs. 265–269. *T. excavata*. 265. Habitus. 266. Head. 267. Genital plates, caudoventral view. 268. Spermatheca. 269. Spermathecal pump.

membranes hyaline, lacking brown flecks. Connexiva narrowly exposed, pale green; posterolateral angles of segments minutely marked with black.

Ventral surface glossy, pale yellow to pale green; punctures concolorous with surface; rostrum pale brown with dark brown markings, apical half of segment 4 piceous, reaching onto base of third (second visible) abdominal sternite. Ostiolar canals acuminate apically. Femora and tibiae pale green. Postspiracular black spots absent; posterolateral angles of abdominal segments minutely marked with black.

Mesial margins of basal plates in caudoventral view nearly straight; posterior margins slightly convex; posteromesial angle of each basal plate distinctly excavated; concavity resulting from excavations in basal plates wider than long, with lateral sides parallel or slightly convergent apically (Fig. 267); surface of basal plates weakly rugose. Sclerotized rod swollen subapically, abruptly narrowed apically (Fig. 268). Spermathecal duct only slightly swollen and coiled below proximal flange (Fig. 269). Male unknown.

Measurements. Total length 8.52–8.99 (8.99); total width 5.13–5.68 (5.68); medial

length of pronotum 1.66–1.89 (1.89). Medial length of scutellum 3.53–3.59 (3.59); basal width 3.20–3.42 (3.42); width at distal end of frena 1.21 (1.21). Length of head 1.68–1.72 (1.72); width 2.14–2.21 (2.21). Length of segments 1–5 of antennae 0.40 (0.40), 0.85–0.88 (0.85), 0.92–1.09 (1.09), 1.10, and 1.14, respectively. Length of segments 2–4 of rostrum 1.31–1.44 (1.44), 0.78–0.92 (0.92), and 0.81–0.86 (0.86), respectively.

Holotype. ♀ labeled (a) "COLOMBIA: Dept. Magdalena,Socorpa Mission,Sierra de Perija, m. VIII-5–25-1968" (b) "Borys Malkin Collector." Deposited in the American Museum of Natural History (New York).

Paratype. 1♀. (a) "Venezuela - AR El Limon 450m 1-VI-1965" (b) "Col. E. Osuna" (c) "Venezuela-Inst Zool.Agricola-Fac.Agronomia Univ, Central" (♀ IZA).

Distribution. Northern South America (Map 3).

Comments. Of the three species of *Thyanta* with distinctly excavated basal plates, *T. excavata* can be identified by the wider than long concavity in the basal plates which has the lateral sides parallel or slightly convergent; and by the weakly rugose surface of the basal plates.

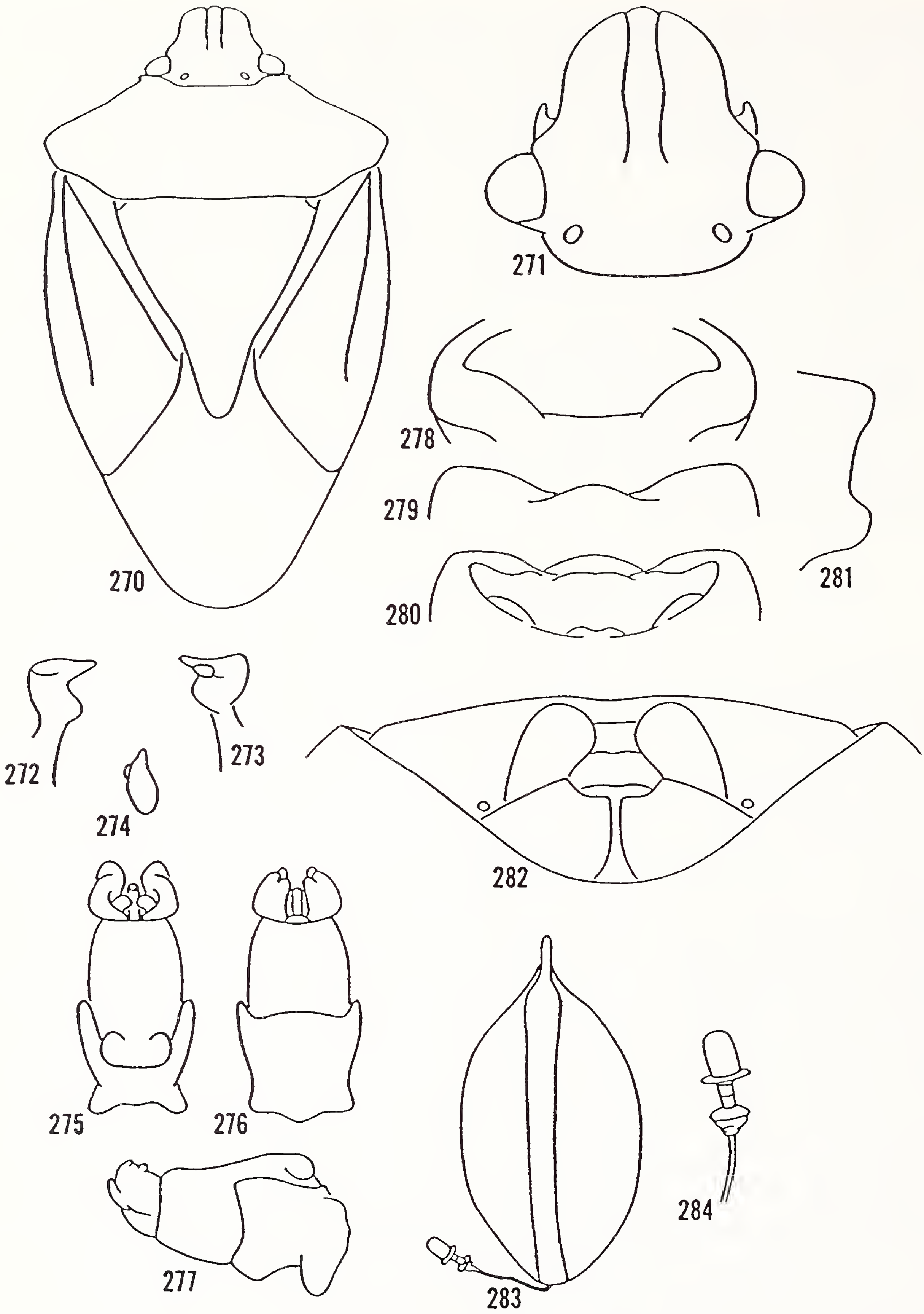
Thyanta (Argosoma) vadosa Rider, new species
Figs. 270–284, Map 3

Description. Ovate; dorsal surface green to pale brown; some interstitial areas of pronotum, scutellum, and elytra pale yellow; sometimes marked with reddish-purple between humeral angles, on apex of scutellum, and on tylus and vertex of head. Punctures green to pale brown.

Apex of head arcuately rounded; outer jugal margins sinuous, subparallel for middle third of distance from eyes to apex (Fig. 271); vertex convex. Antennae pale green to brown, apical portions of distal 3 segments reddish to dark brown. Anterolateral margins of pronotum in dorsal view straight to slightly concave; humeral angles rounded to angulate, often projecting beyond base of adjacent coria (Fig. 270). Pronotal cicatrices immaculate. Punctation becoming sparse medially, central portion of pronotal disc subcalloused. Posterior third of pronotum often darker than rest of pronotum. Basal disc of scutellum tumid. Hemelytra glossy, punctures shallow, uniformly distributed; costal angles narrowly rounded to angulate, reaching to middle of penultimate connexival segments. Membranes hyaline, with a few obsolescent brown flecks distally. Connexiva narrowly exposed, green to pale brown, posterolateral angles of segments piceous.

Venter pale yellow to green; punctures concolorous. Femora and tibiae pale brown to green, tarsal segments and apex of each tibia darker. Rostrum green to pale brown, distal half of segment 4 black, reaching onto base of abdomen. Ostiolar canals acuminate apically. Postspiracular black spots lacking (except in brown form); posterolateral angles of abdominal sternites marked with piceous, sometimes only minutely so.

Mesial margins of basal plates in caudoventral view straight to slightly convex; posterior margins slightly convex; posteromesial angle of each basal plate broadly and shallowly emarginate, lateral sides of concavity resulting from excavations in basal plates divergent, not parallel (Fig. 282). Distal end of sclerotized rod swollen subapically, narrowed apically (Fig. 283); spermathecal duct moderately swollen and coiled below proximal flange (Fig. 284). Posterior margin of pygophore in caudal



Figs. 270–284. *T. vadosa.* 270. Habitus. 271. Head. 272–274. Right paramere. 272. Medial view. 273. Lateral view. 274. Ectal view. 275–277. Theca and related structures. 275. Ventral view. 276. Dorsal view. 277. Lateral view. 278–281. Pygophore. 278. Caudal view. 279. Ventral view. 280. Dorsal view. 281. Lateral view. 282. Genital plates, caudoventral view. 283. Spermatheca. 284. Spermathecal pump.

view broadly U-shaped, medial portion straight to slightly convex (Fig. 278); chin-like protuberance appearing relatively narrow in ventral and dorsal views (Figs. 278, 279); pygophore deeply emarginate in lateral view (Fig. 281). Each paramere with concave surface oriented mediad; from ectal view, apex angling gently mesad (Fig. 274); from medial view, apex acutely angulate, straight or bending slightly ventrad (Fig. 272); roughened spiculate area on lateral surface ovoid (Fig. 273). Each lateral conjunctival lobe of aedeagus without sclerotized diverticula (Fig. 277); dorsomedial conjunctival lobe weakly developed (Fig. 276); median penial lobes spatulate (Fig. 275).

Measurements. Total length 7.57–10.17 (8.04); total width 4.73–6.15 (5.05); medial length of pronotum 1.60–1.88 (1.66). Medial length of scutellum 3.15–4.08 (3.42); basal width 2.98–3.75 (3.20); width at distal end of frena 1.14–1.32 (1.18). Length of head 1.59–1.86 (1.64); width 2.12–2.39 (2.21). Length of segments 1–5 of antennae 0.44–0.52 (0.44), 0.81–0.96 (0.85), 0.96–1.14 (1.07), 1.14–1.25 (1.14), and 1.07–1.18 (1.07), respectively. Length of segments 2–4 of rostrum 1.21–1.44 (1.29), 0.74–0.88 (0.77), and 0.70–0.81 (0.74), respectively.

Holotype. ♂ labeled (a) "Santa Margarita Hill, TRINIDAD May, 1959" (b) "Taken at light." Deposited in the Canadian National Collection, Ottawa, Canada.

Paratypes. 5♂♂, 5♀♀. "Trinidad, W.I. Sept. 58–June 59" (♂ CNC); (a) "Bejucal, Trinidad,BWI, 24 Oct. 1945" (b) "E. McC. Callan Collector" (c) "on inflorescences of Cordia macrostachya" (♂ USNM); (a) "Trinidad, 8 II '52, F. Schrader, ♂, 776" (b) "Thyanta pseudocasta (Blt.) cp. with TYPE, det. Ruckes" (♂ AMNH); "TOBAGO: W.I. 17–19 July 1964 J.M. Capriles" (♂ USNM); (a) "TRINIDAD: Curepe, Santa Margarita Circular Rd. 5-III-76 F. D. Bennett blacklight trap" (b) "C J Drake Coll. 1956" (♂ USNM); TRINIDAD: Curepe, Santa Margarita Circular Rd. III-19-75-X-1971 F. D. Bennett, Blacklight trap" (2♀♀ ARH); (a) "St. Augustine, Trinidad, BWI, Sept. 15, 1944" (b) "I. E. Kirby Coll." (c) "I.C.T.A. 12953" (♀ USNM); (a) "Trinidad, 16 I '52, F. Schrader, 702" (b) "Thyanta maculata (Fabr.), det H. Ruckes" (♀ AMNH); and "VENEZUELA: Lara; Yacambu National Park 13kmSE Sanare,4800 feet, 4–7 III 1978,blacklight, cloud forest,J.B.Heppner" (♀ USNM).

Distribution. Trinidad and Tobago; Venezuela (Map 3).

Comments. The shape of the emargination in the posteromesial angle of each basal plate of the female is distinctive. *Thyanta emarginata* and *T. excavata* both have the posteromesial angles of the basal plates deeply emarginate, but the sides of the resulting concavity are nearly parallel, not divergent as in *T. vadosa.* The male genitalia are also distinctive. *Thyanta vadosa* is the only species with the apex of each paramere not only acutely angulate (almost acuminate) but also straight or bending slightly ventrad. All other species in the subgenus *Argosoma* that have the apex of each paramere acute to acuminate also have the apex bending dorsad.

Etymology. Vadosa is the Latin word for shallow. This species is named for the distinct but shallow excavation of the posteromesial angle of each basal plate.

Thyanta (Argosoma) curvata Rider, new species
Figs. 285–299, Map 1

Description. Medium to large; dorsal surface pale green to pale brown, female specimens usually with reddish transhumeral markings in form of oblong spot on

each side of middle and smaller spot near apex of each humeral angle, sometimes apex of scutellum also reddish; punctures usually concolorous with surface.

Apex of head narrowly rounded; outer jugal margins not parallel (Fig. 286). Antennae pale green to pale brown, sometimes distal portions of last three segments darker. Anterolateral margins of pronotum straight to slightly concave in dorsal view; humeral angles narrowly rounded, almost angulate, protruding beyond base of adjacent coria by one-half width of eye or less (Fig. 285); pronotal cicatrices immaculate. Hemelytra shallowly and uniformly punctate; posterior margins straight to slightly convex; posterolateral angles narrowly rounded, ending above penultimate connexival segments; hemelytral membranes hyaline, lacking distal brown flecks. Connexiva usually narrowly exposed; incisures usually minutely tipped with black.

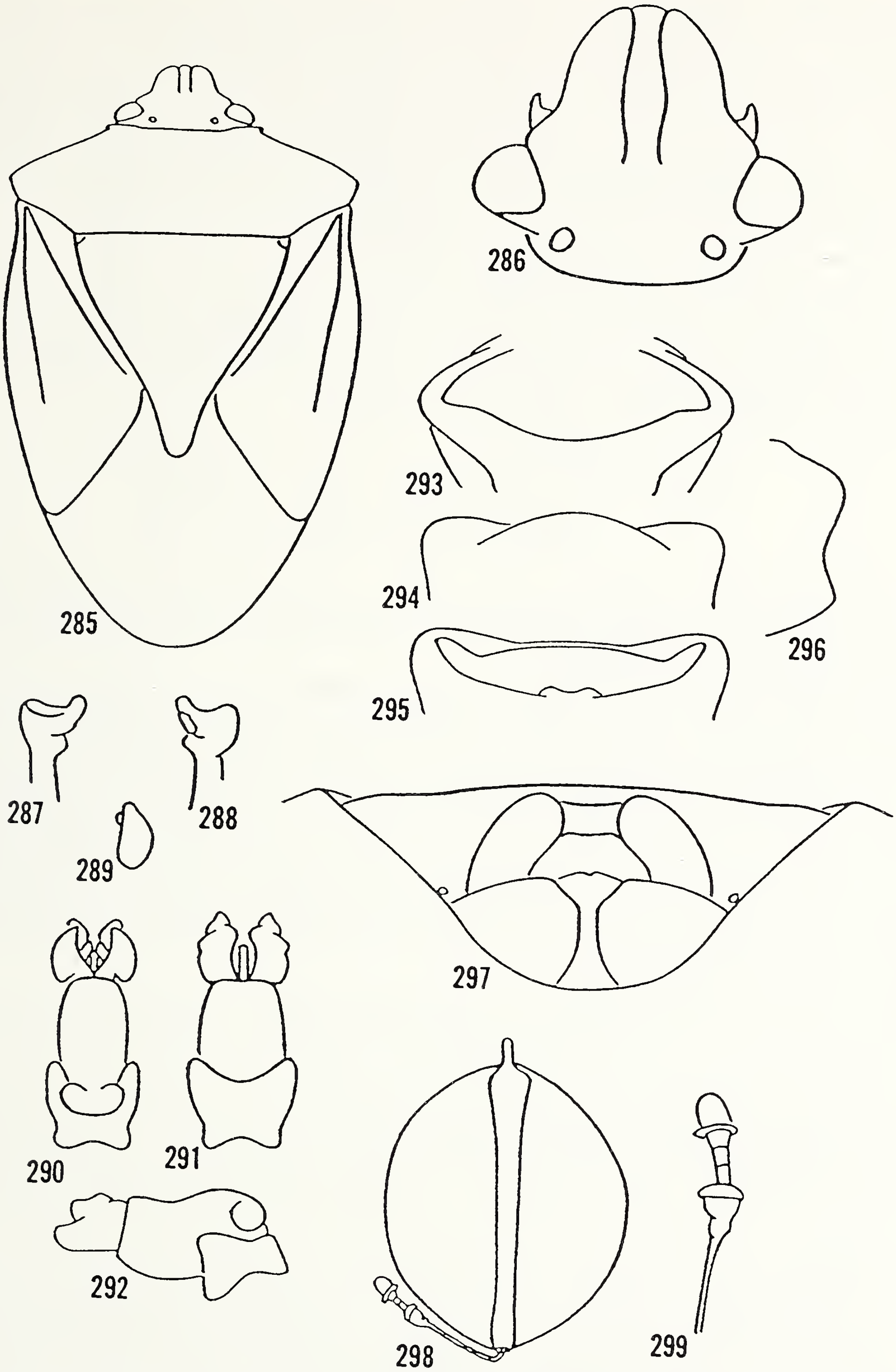
Ventral surface pale yellowish-green to brown; punctures concolorous with surface. Rostrum green to pale brown, apical half of segment 4 piceous; reaching onto third (second visible) abdominal sternite. Ostiolar canals acuminate apically. Femora and tibiae green to brown; tarsi and distal portions of tibiae sometimes darker. Postspiracular black spots lacking; posterolateral angles of abdominal sternites piceous.

Mesial margins of basal plates in caudoventral view straight to slightly convex; posterior margins slightly convex; posteromesial angles slightly emarginate (Fig. 297). Sclerotized rod swollen subapically, distinctly narrowed apically (Fig. 298). Spermathecal duct moderately swollen below proximal flange, without coiling from swollen area to sclerotized rod (Fig. 299). Posterior margin of pygophore in caudal view broadly and shallowly U-shaped, medial portion straight to slightly concave, sinuous (Fig. 293); blunt, chin-like protuberance prominent in ventral view (Fig. 294); posterior margin broadly U-shaped in dorsal view (Fig. 295); pygophore concave in lateral view (Fig. 296). Concave surface of each paramere oriented more dorsad than mediad; in medial view apex short, rounded, distinctly bent dorsad (Fig. 287); in ectal view, apex bluntly rounded (Fig. 289); roughened, spiculate area on lateral surface ovoid (Fig. 288). Each lateral conjunctival lobe of aedeagus with 1–2 narrowly rounded diverticula (Fig. 292); dorsomedial lobe lacking (Fig. 291); median penial lobes and penisfilum relatively small, obscured by conjunctival membranes (Fig. 290).

Measurements. Total length 6.78–8.75 (6.75); total width 4.57–5.83 (4.57); medial length of pronotum 1.50–1.73 (1.50). Medial length of scutellum 2.94–3.61 (2.94); basal width 2.80–3.53 (2.80); width at distal end of frena 0.96–1.25 (0.96). Length of head 1.46–1.68 (1.46); width 1.88–2.23 (1.88). Length of segments 1–5 of antennae 0.35–0.44 (0.44), 0.75–0.96 (0.86), 0.77–0.99 (0.77), 0.96–1.10 (0.96), and 0.96–1.10 (0.96), respectively. Length of segments 2–4 of rostrum 1.14–1.32 (1.18), 0.77–0.88 (0.77), and 0.74–0.81 (0.74), respectively.

Holotype. ♂ labeled (a) "El Limon AR VENEZUELA 450m. 31-V-57" (b) "F.Fernandez Y., C. J. Rosales Cols." (c) "Venezuela-Inst. Zool.Agricola-Fac.Agronomia Univ. Central." Deposited in the Universidade Central de Venezuela (Maracay).

Paratypes. 6♂♂, 11♀♀. Labeled same as holotype (5♂♂/3♀♀ IZA); (a) "Mariara Venezuela, Carabobo 460m. 12-II-1967" (b) "Trampa de luz" (c) "L.Fernandez S. col." (d) "Venezuela-Inst. Zool.Agricola-Fac.Agronomia Univ. Central" (♀ IZA); (a) "Galeras del Pao COJEDES Venezuela 26-IV-1963" (b) "C.J.Rosales A. Perez" (c) "Venezuela-Inst. Zool.Agricola-Fac.Agronomia Univ. Central" (♀ IZA); "VENEZUELA:



Figs. 285–299. *T. curvata.* 285. Habitus. 286. Head. 287–289. Right paramere. 287. Medial view. 288. Lateral view. 289. Ectal view. 290–292. Theca and related structures. 290. Ventral view. 291. Dorsal view. 292. Lateral view. 293–296. Pygophore. 293. Caudal view. 294. Ventral view. 295. Dorsal view. 296. Lateral view. 297. Genital plates, caudoventral view. 298. Spermatheca. 299. Spermathecal pump.

Aragua 2kmN OcumareDeLa Costa,21–22-VI-1976 A.S.Menke&D.Vincent" (♀ USNM); (a) "Venezuela-Barinas. Reserva Forestal-Ticoporo. 230m 3–10-IV-66" (b) "F. Fernandez. Y Luis.J.July" (c) "Venezuela-Inst Zool.Agricola-Fac.Agronomia Univ. Central" (3♀♀ IZA); "RioFrio Colombia S.A.2-VII-1926 George Salt" (♀ USNM); (a) "El Sombrero Cenarico, Venz. 29-IV 1953" (b) "Col. J. Requena" (c) "Venezuela-Inst Zool.Agricola-Fac.Agronomia Univ. Central" (♀ IZA); and "VENEZUELA: Zulia Carrasquero 29–30 May 1976 A.S.Menkee&D.Vincent" (♂ USNM).

Distribution. Northern South America (Map 1).

Comments. Some female specimens of this species closely resemble maculate individuals of the Central American species *T.* (*A.*) *maculata* (F.). The male genitalia are distinctive, as no other congener has the apex of each paramere short, rounded, and curving dorsad in medial view as in this species.

Etymology. Named for the distinctly curved apex of each paramere.

Thyanta (Argosoma) sinuata Rider, new species
Figs. 300–307, Map 2

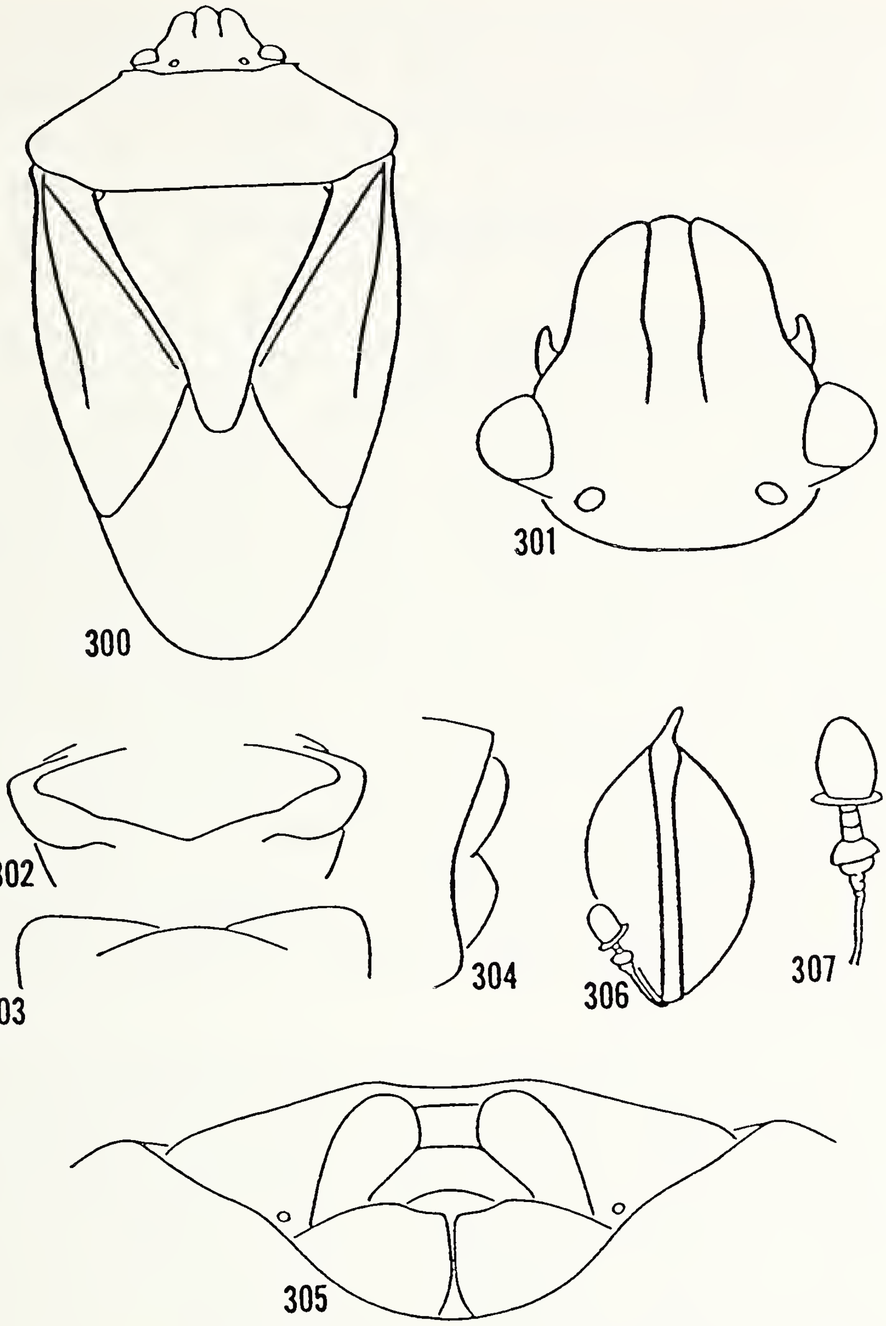
Description. Small to medium; dorsal surface pale yellowish-green, lacking all red or black markings; punctures slightly darker than surface, sparse everywhere except along anterior margin of pronotum.

Apex of head narrowly rounded; outer jugal margins not quite parallel (Fig. 301). Antennae pale brown, distal 3 segments darker. Anterolateral margins of pronotum in dorsal view almost straight, nearly devoid of punctures submarginally; humeral angles rounded, protruding only slightly beyond base of adjacent coria (Fig. 300); pronotal cicatrices immaculate. Hemelytra shallowly and sparsely punctate; posterior margins slightly convex; costal angles narrowly rounded, reaching to near posterior margin of penultimate connexival segments; hemelytral membranes hyaline with a few distal brown flecks. Connexiva usually narrowly exposed, incisures sometimes minutely marked with piceous.

Ventral surface yellowish-brown; posterolateral angles of abdominal sternites immaculate; postspiracular black spots lacking. Rostrum pale yellowish-green, apical half of segment 4 piceous, extending onto base of abdomen; femora and tibiae green to brown, tarsal segments sometimes darker. Ostiolar canals acuminate apically.

Mesial margins of basal plates in caudoventral view convex; posterior margins sinuous; posteromesial angles shallowly emarginate (Fig. 305). Distal end of sclerotized rod swollen subapically, narrowed apically (Fig. 306); spermathecal duct with small amount of swelling and coiling below proximal flange (Fig. 307). Posterior margin of pygophore in caudal view shallowly and sinuously V-shaped (Fig. 302); posteroventral surface only feebly produced into blunt, chin-like protuberance in ventral view (Fig. 303); emarginate in lateral view (Fig. 304). Concave surface of each paramere oriented dorsomediad; each paramere robust; in medial view apex broad, nearly angulate, not curving dorsad.

Measurements. Total length 6.62–7.89 (6.62); total width 4.49–5.50 (4.49); medial length of pronotum 1.25–1.55 (1.25). Medial length of scutellum 2.86–3.31 (2.86); basal width 2.80–3.09 (2.80); width at distal end of frena 0.96–1.10 (0.96). Length of head 1.46–1.59 (1.46); width 1.94–2.12 (1.94). Length of segments 1–5 of antennae 0.37 (0.37), 0.74–0.79 (0.74), 0.88–0.92 (0.92), 0.96–0.98 (0.96), and 0.92–0.96 (0.92),



Figs. 300–307. *T. sinuata.* 300. Habitus. 301. Head. 302–304. Pygophore. 302. Caudal view. 303. Ventral view. 304. Lateral view. 305. Genital plates, caudoventral view. 306. Spermatheca. 307. Spermathecal pump.

respectively. Length of segments 2–4 of rostrum 1.18–1.21 (1.18), 0.70–0.72 (0.70), and 0.66–0.68 (0.66), respectively.

Holotype. ♂ labeled (a) "COLOMB Magdal. Santa Marta X-8-71 GEBohart" (b) "Thyanta signoreti Ruckes LHR 74." The holotype specimen is in poor condition having the abdomen partially loose from the rest of the body. Deposited in the U.S. National Museum of Natural History (Washington, D.C.).

Paratypes. 1♂, 2♀♀. Labeled same as holotype except lacking (b) (♀ DAR, ♀ LHR); and (a) "Acarigua Est. Portuguesa Ven. VI-81" (b) "C J Drake Coll. 1956" (♂ USNM).

Distribution. Colombia and Venezuela (Map 2).

Comments. The form of the posterior pygophoral margin and the structure of the

parameres are unique within the genus. The sparse overall punctation will also help identify this species. Due to the poor condition of the holotype, the male genitalia were not dissected, but the characters of the parameres are visible without dissection.

Etymology. Named for the sinuously V-shaped posterior margin of the pygophore.

Thyanta (Argosoma) obtusa Rider, new species
Fig. 308–321, Map 3

Description. Small to medium; dorsal surface pale green to testaceous, lacking all red and black markings; punctures usually concolorous with surface.

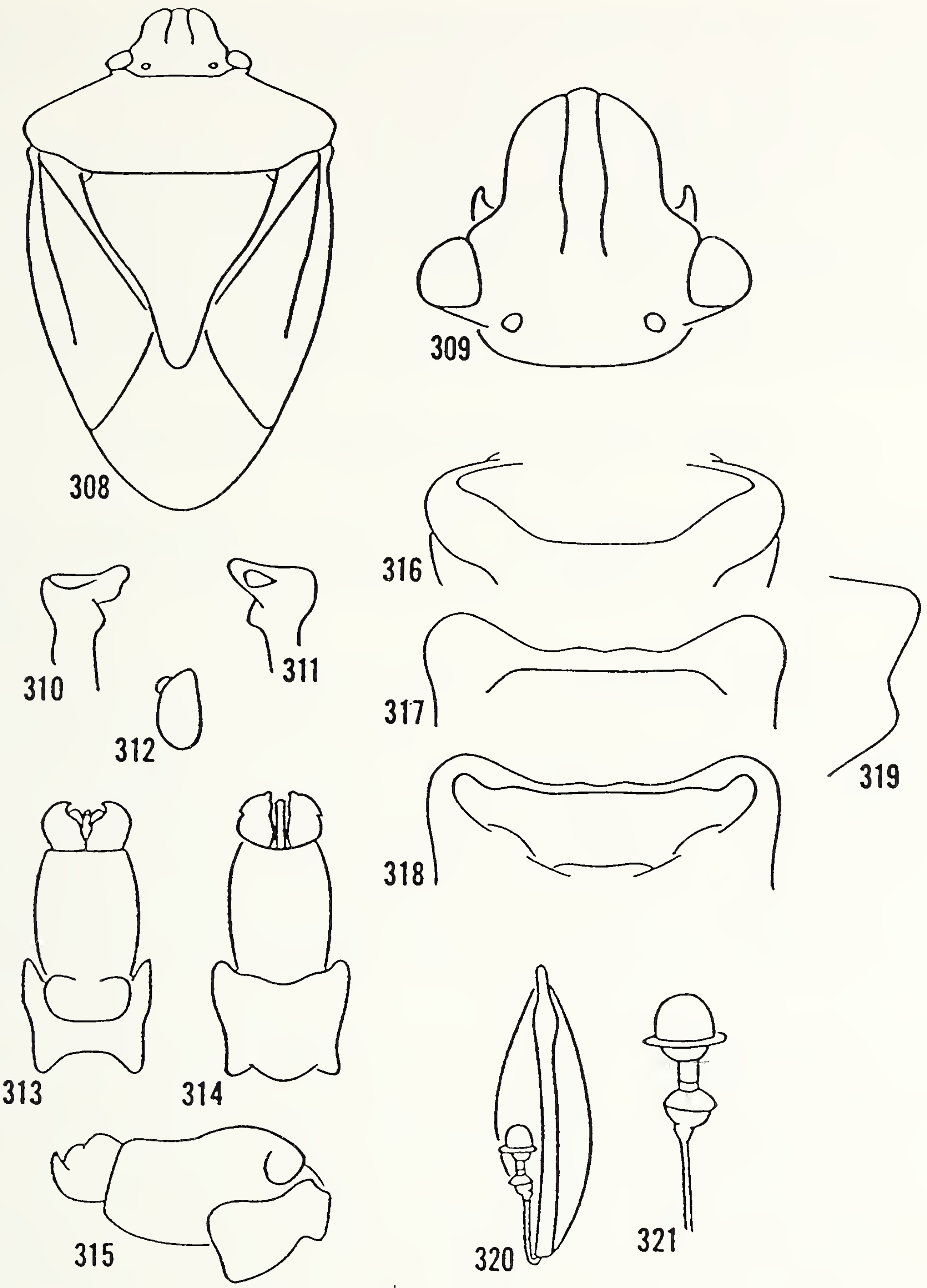
Apex of head arcuately rounded; outer jugal margins subparallel for middle third of distance from eyes to apex (Fig. 309). Antennae pale brown, apical 3 segments sometimes reddish-brown. Anterolateral margins of pronotum straight to slightly concave in dorsal view; humeral angles rounded, protruding only slightly beyond base of adjacent coria (Fig. 308); pronotal cicatrices immaculate. Hemelytra shallowly and uniformly punctured; posterior margins slightly convex; costal angles narrowly rounded, reaching beyond middle of penultimate connexival segments; hemelytral membranes hyaline, usually with a few vague brown flecks distally. Connexiva narrowly exposed; incisures sometimes minutely marked with black.

Ventral surface yellowish-green to brown; punctures usually concolorous with surface. Rostrum pale green to brown, apical half of segment 4 black; usually reaching onto third (second visible) abdominal segment. Femora and tibiae green to brown, sometimes tarsal segments darker. Ostiolar canals acuminate apically. Postspiracular black spots absent; posterolateral angles of abdominal sternites usually immaculate, extreme tip sometimes black.

Mesial margins of basal plates nearly straight; posterior margins sinuous; posteromesial angles rounded. Sclerotized rod slightly swollen subapically, narrowed apically (Fig. 320); spermathecal duct below proximal flange with only slight amount of swelling or coiling (Fig. 321). Posterior margin of pygophore shallowly and broadly U-shaped, medial portion straight to slightly convex in caudal view (Fig. 316); posterolateral angles prominent in ventral and lateral views (Figs. 317, 319); blunt, chinlike protuberance on posteroventral surface relatively small, not visible in dorsal view (Fig. 318). Each paramere in ectal view relatively robust, apex obtuse (Fig. 312); in medial view apex rounded, curving only slightly dorsad, concave surface oriented more dorsad than mediad (Fig. 310); distinct obtuse protuberance on shaft; roughened, spiculate area on lateral surface circular or triangular (Fig. 311). Each lateral conjunctival lobe of aedeagus with 1–2 nonsclerotized diverticula (Fig. 315); dorsomedial lobe apparently lacking (Fig. 314); penisfilum and median penial lobes nearly obscured by conjunctival membrane (Fig. 313).

Measurements. Total length 6.86–7.73 (6.86); total width 4.42–5.20 (4.42); medial length of pronotum 1.36–1.62 (1.47). Medial length of scutellum 2.96–3.15 (2.98); basal width 2.80–3.09 (2.83); width at distal end of frena 1.03–1.10 (1.03). Length of head 1.46–1.59 (1.46); width 1.92–2.13 (1.92). Length of segments 1–5 of antennae 0.37–0.42 (0.37), 0.70–0.92 (0.70), 0.83–1.03 (0.92), 1.05–1.20 (1.05), and 1.03–1.18 (1.03), respectively. Length of segments 2–4 of rostrum 1.12–1.23 (1.12), 0.68–0.79 (0.68), and 0.72–0.77 (0.72), respectively.

Holotype. ♂ labeled (a) "Villa Vieja Colombia 11-IV-45" (b) "Thyanta nitidula



Figs. 308–321. *T. obtusa.* 308. Habitus. 309. Head. 310–312. Right paramere. 310. Medial view. 311. Lateral view. 312. Ectal view. 313–315. Theca and related structures. 313. Ventral view. 314. Dorsal view. 315. Lateral view. 316–319. Pygophore. 316. Caudal view. 317. Ventral view. 318. Dorsal view. 319. Lateral view. 320. Spermatheca. 321. Spermathecal pump.

Ruckes det. H. Ruckes." Deposited in the California Academy of Sciences (San Francisco).

Paratypes. 4♂♂, 1♀. "Magdalena, Colom. 11°10'N, 76°08'W Apr. 1973, 800 M M. Madison, Coll." (2♂♂ LHR); (a) "Trujillo Trujillo, Venz. 12-VII-1964" (b) "E. Osuna M. Gelbes" (c) "Venezuela-Inst. Zool. Agricola-Fac, Agronomia Univ. Central" (♂ IZA); (a) "El Limon Ar. VENEZUELA 450m. 30-V-65" (b) "F. Fernandez Y. Col."

(c) "Venezuela-Inst. Zool. Agricola-Fac, Agronomia Univ. Central" (♂ IZA); and (a) "Turmero; AR Venezuela 466 m 22.V.53" (b) "col. J. Requena" (c) "Venezuela-Inst Zool.Agricola-Fac.Agronomia Univ. Central" (♀ IZA).

Distribution. Northern South America (Map 3).

Comments. This species is related to *T. sinuata* and *T. xerotica,* but can be recognized by the structure of the male genitalia. *Thyanta obtusa* has the posterior margin of the pygophore broadly U-shaped in caudal view, while in *T. sinuata* it is broadly V-shaped. *Thyanta obtusa* can be separated from *T. xerotica* by the obtuse protuberance on the shaft of each paramere, which is reduced or absent in *T. xerotica.*

Etymology. Named for the obtuse apex of each paramere when viewed medially.

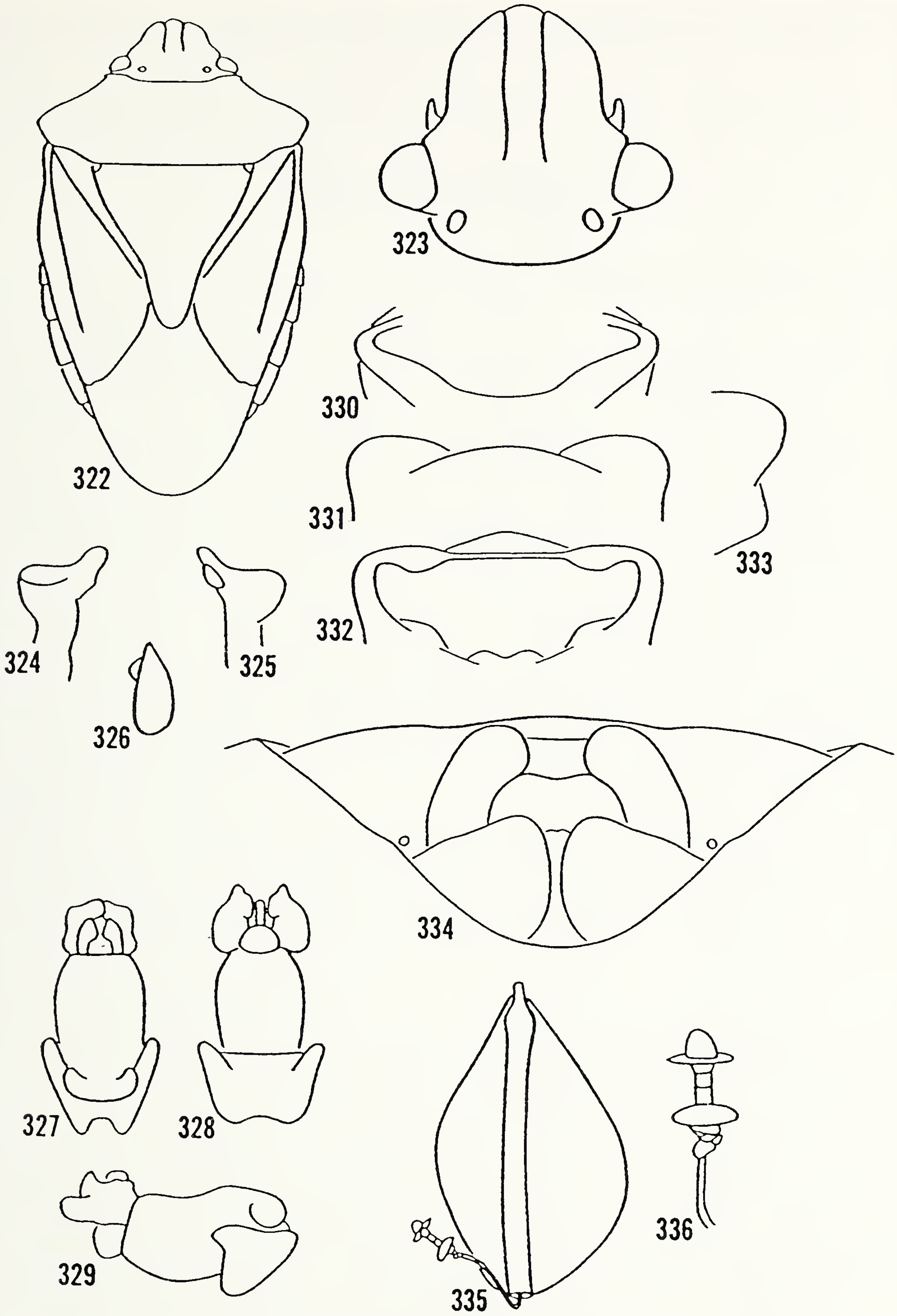
Thyanta (Argosoma) xerotica Rider, new species
Figs. 322–336, Map 2

Description. Medium to large; dorsal surface green to brown; often with reddish markings between humeral angles, on apex of scutellum, and sometimes on vertex of head and apices of coria; punctures usually concolorous with surface, sometimes brown.

Outer jugal margins subparallel for middle third of distance from eyes to evenly rounded apex (Fig. 323). Antennae green to pale brown, distal 3 segments usually marked with dark brown or reddish-brown. Anterolateral margins of pronotum in dorsal view straight to slightly concave; humeral angles rounded to nearly angulate, protruding only slightly beyond base of adjacent coria (Fig. 322); pronotal cicatrices immaculate. Hemelytra uniformly and densely punctate; posterior margins slightly convex; costal angles narrowly rounded to angulate, reaching beyond middle of penultimate connexival segments; hemelytral membranes hyaline, sometimes with numerous brown flecks. Connexiva narrowly exposed; incisures usually marked with black.

Ventral surface green to pale brown; punctures usually concolorous with surface; humeral angles often marked with black. Rostrum green to brown, apical half of segment 4 piceous, apex reaching beyond middle of third (second visible) abdominal segment. Ostiolar canals acuminate apically. Femora and tibiae green to brown, tarsal segments and apex of each tibia often darker. Postspiracular black spots absent, sometimes vague in brown form; posterolateral angles of abdominal sternites piceous.

Mesial margins of basal plates in caudoventral view straight to slightly convex, separated basally; posterior margins sinuous, nearly straight; posteromesial angles broadly rounded (Fig. 334). Sclerotized rod relatively short, somewhat swollen subapically, distinctly narrowed apically (Fig. 335); spermathecal duct only slightly swollen and coiled below proximal flange (Fig. 336). Medial portion of posterior pygophoral margin in caudal view usually concave, continuing line of lateral margins, giving posterior margin a smoothly arcuate form, medial portion sometimes straight and posterior margin more U-shaped (Fig. 330); pygophore emarginate in lateral view (Fig. 333); posterolateral angles moderately prominent in both ventral and dorsal views (Figs. 331, 332). Each paramere relatively robust, concave surface oriented dorsomediad, apex rounded in medial view (Fig. 324), angulate in ectal view (Fig. 326), roughened, spiculate area on lateral surface localized, ovoid (Fig. 325). Each lateral conjunctival lobe of aedeagus with 2 diverticula (Fig. 329); dorsomedial conjunctival lobe prominent (Fig. 328); penisfilum relatively small (Fig. 328).



Figs. 322–336. *T. xerotica.* 322. Habitus. 323. Head. 324–326. Right paramere. 324. Medial view. 325. Lateral view. 326. Ectal view. 327–329. Theca and related structures. 327. Ventral view. 328. Dorsal view. 329. Lateral view. 330–333. Pygophore. 330. Caudal view. 331. Ventral view. 332. Dorsal view. 333. Lateral view. 334. Genital plates, caudoventral view. 335. Spermatheca. 336. Spermathecal pump.

Measurements. Total length 6.62–10.25 (7.41); total width 4.34–6.47 (4.73); medial length of pronotum 1.40–1.88 (1.49). Medial length of scutellum 2.72–4.25 (3.13); basal width 2.61–4.08 (2.94); width at distal end of frena 0.94–1.32 (1.05). Length of head 1.55–2.07 (1.68); width 1.99–2.65 (2.13). Length of segments 1–5 of antennae 0.40–0.52 (0.44), 0.71–1.10 (0.88), 1.07–1.42 (1.14), 1.18–1.49 (1.47), and 1.14–1.38 (1.31), respectively. Length of segments 2–4 of rostrum 1.25–1.69 (1.42), 0.70–0.92 (0.77), and 0.77–0.99 (0.77), respectively.

Holotype. ♂ labeled "Guayaquil Ecua 1940 CLFagen." Deposited in the U.S. National Museum of Natural History (Washington, D.C.).

Paratypes. 28♂♂ and 25♀♀. "Ecuador Manabi San Clemente VII 84 Legit: F. Cuesta" (♂ 2♀♀ QCAZ); "ECUADOR, 82 Km. W. Guayaquil Ricklefs & Austin 8 March 77" (2♂♂ DBT); (a) "Guayaquil Ecuador RL Castillo" (b) "Thyanta nitidula Ruckes det H. Ruckes" (♀ CU); (a) "ECUADOR La Toma 1200m. W.Loja 18,19-XI-1970 Coll:L.E.Pena" (b) "33" (♂ DAR); (a) "Peru S.A. I.23 1936 E.G.Smyth" (b) J.R.de la Torre-Bueno Collection K.U." (4♂♂ 7♀♀ SMEK), except 3♂♂ labeled "I.25 1936," 1♂ labeled "III.14 1937," 1♀ labeled "III.15 1937," and 2♀♀ labeled "III.16 1937"; (a) "Lima, Peru Feb. 2, 1939 Carl J. Drake" (b) "C J Drake Coll. 1956" (♂ USNM); "Peru. Dpto. Amazonas 43 K. ne. Chikiaco 1050′ 6–10 XI 1978 L. J. Barkley" (♂ LHR); (a) "PERU:Dept. Cajamarca Prov. Jaén. Pucara. Rio Huancabamba,900m 14–18.I.1964" (b) "P. C. Hutchison and J. K. Wright Collectors" (♂ 4♀♀ CAS), except 1♂ labeled "10–13.I.1964"; "PERU: Dpto. Lambayeque Cerro la Vieja, 7 km. S of Motupe, el. 100m. 2-17-VII-1981 L.J.Barkley, collector" (♂ LHR); (a) "10 Km.S.of Chiclayo, PERU III-21-51" (b) "Ross and Michelbacher Collectors" (♀ CAS); "PERU: Dpto. Lambayeque 12 km. N of Olmos el. 90m. 1-VII-81 L.J. Barkley, coll." (2♂♂ LHR); (a) "PERU:Dept. & Prov. Lambayeque. 18 km. W. of Olmos. Alt. 520m 30-IX-1964" (b) "P. C. Hutchison & J. K. Wright At Coleman lantern" (♂ ♀ CAS); (a) "PERU: 94 mi. E. of Olmos, Lambayeque I-18-1955" (b) "E.I.Schlinger & E.S.Ross collectors" (♂ CAS); (a) "PERU: Lambayeque. Roadside veg. 1 mile S.E. of town. 20.viii.1971." (b) "Fertile irrigated region in arid coastal desert" (c) "P.S.&H.L. Broomfield B.M. 1971-486 (2♂♂ BMNH); (a) "Chaclacayo Lima,Peru 750Meters" (b) "Acc.38901 E.Escomel" (♀ AMNH); (a) "LIMA PERU 1959 F.Cisneros Col." (b) "UA 696-67" (♂ DAR); (a) "Lima Peru VI-1-39 Weyrauch 91" (b) "Thyanta patruelis Stal det H. Ruckes" (♀ USNM); "PERU: Dpto. Piura Pariñas, 7 km. N, 15 km. E Talara 18-IX-1981 L.J. Barkley, coll." (♂ LHR); (a) "PERU: Dept. Piura, Prov. Ayabaca. 18 km above Puente Tandopa (RioQuiróz)" (b) "Alt. 1000–1700 m. 23-IX-1964 P. C. Hutchison & J. K. Wright" (♀ CAS); "Tamarugal Refresco Enero 16, 1986 D. Bobadilla" (4♂♂ UTAC); "Tamarugal Enero 30, 86 D. Bobadilla" (♂ UTAC); "Tamarugal Enero 30, 86 A. Gallardo" (♀ UTAC); (a) "4" (b) "PAMPA-TAMARUGAL-16-07-86 D. BOBADILLA colector" (♂ IIAS); "CHILE-Arica 19.09.82 Trampa tablero Col. C. Valdés" (♀ IIAS); (a) "5" (b) "TARAPACA CICA.AZAPA LUZ-NEGRA 26–27-I-70" (2♀♀ IIAS), except 1♀ labeled (a) "6"; (a) "Chile, 194 ~~Arg.~~ M. L. Parker" (b) "C J Drake Coll. 1956" (2♂♂ ♀ USNM); and "CHILE. Pica 23.02.84 Vegetación Col. E. Prado" (♀ IIAS).

Distribution. Coastal desert areas from Ecuador to northern Chile (Map 2).

Comments. This species can be distinguished from other congeners by the form of the posterior margin of the pygophore and by the structure of the parameres. The posterior margin of the pygophore in caudal view is usually arcuately U-shaped. *Thyanta xerotica* is the only species of *Thyanta* with the apex of each paramere

distinctly rounded in medial view and usually lacking the obtuse protuberance on the shaft.

Etymology. Named for the xerophytic habitat in which this species lives.

Thyanta (Argosoma) infuscata Rider, new species
Figs. 337–351, Map 2

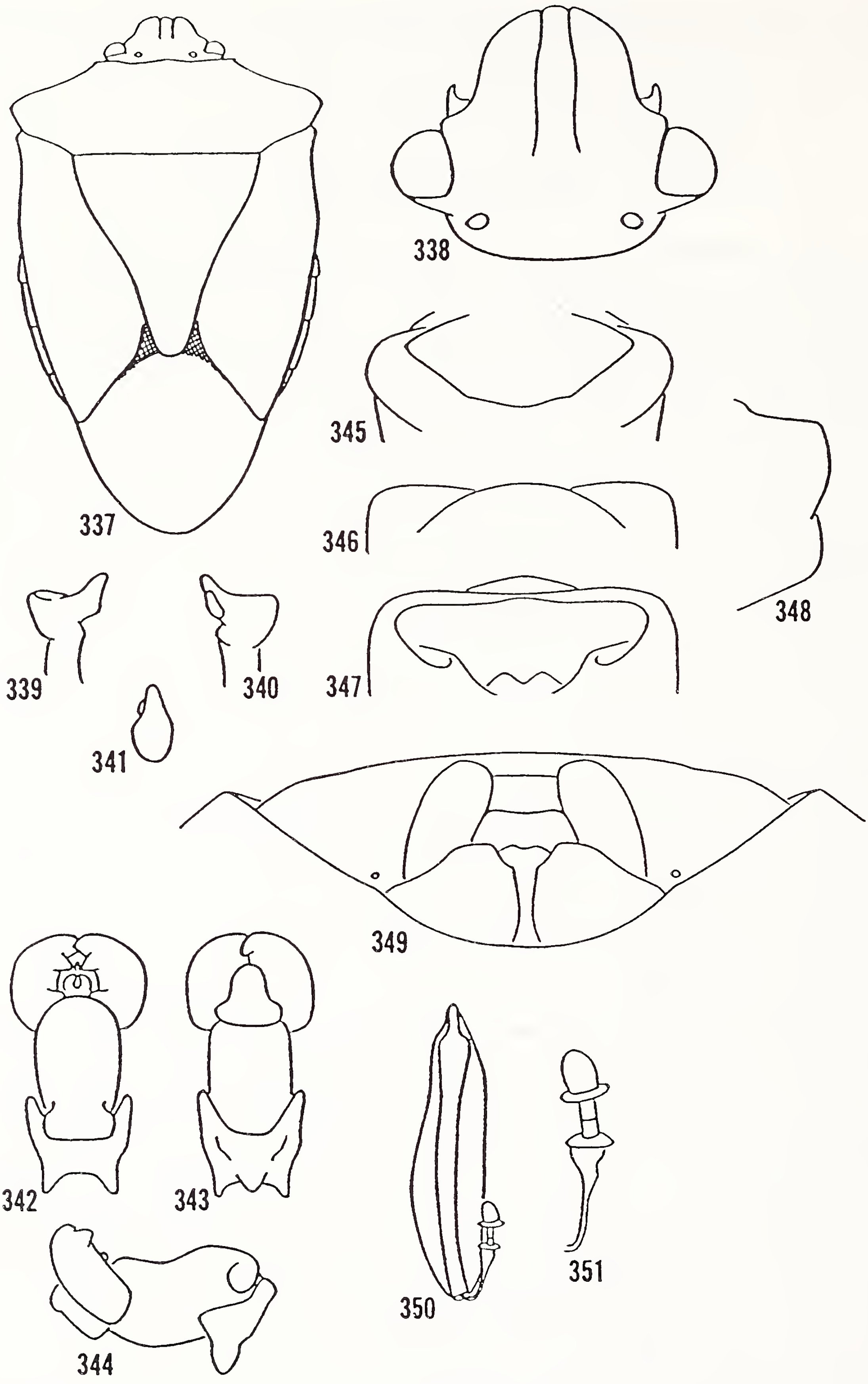
Description. Dorsal surface pale green; posterior third of pronotum dark green, margin between pale and dark areas irregular; medial longitudinal band on scutellum yellowish-green; punctures reddish-brown.

Apex of head broadly rounded; outer jugal margins nearly parallel for middle third of distance from eyes to apex (Fig. 338). Antennae pale reddish-brown, distal two and one-half segments darker. Anterolateral margins of pronotum weakly concave in dorsal view; humeral angles narrowly rounded, almost angulate, produced beyond margin of adjacent coria by about one-half width of eye, piceous apically (Fig. 337). Mesial margin of each pronotal cicatrice marked with fuscous or piceous, sometimes only vaguely so. Punctures on pronotum crowded anterior to cicatrices, sparse along anterolateral margins. Hemelytra uniformly and shallowly punctate, punctures slightly more dense on exocorium than corium; posterior margins nearly straight; posterolateral angles narrowly rounded, extending nearly to posterior margin of penultimate connexival segments. Hemelytral membranes hyaline with numerous brown flecks; inner basal angle distinctly infuscated (Fig. 337). Connexiva pale green; posterolateral angles piceous.

Ventral surface yellowish-green; punctures concolorous to reddish-brown. Rostrum pale yellowish brown, apical half of segment 4 black, reaching onto base of third (second visible) abdominal sternite. Ostiolar canals acuminate apically. Femora and tibiae pale yellowish-green; vague brown spot present on superior surface of each femur at distal third. Postspiracular black spots absent. Posterolateral angles of abdominal sternites piceous.

Mesial margins of basal plates in caudoventral view slightly convex, separated basally; posterior margins slightly concave; posteromesial angles slightly emarginate, fuscous (Fig. 349). Sclerotized rod swollen subapically, abruptly narrowed apically (Fig. 350); spermathecal duct moderately swollen below proximal flange, length of duct from proximal flange to sclerotized rod short relative to congenors (Fig. 351). Posterior margin of pygophore broadly and sinuously U-shaped in caudal view, medial portion slightly sinuous (Fig. 345); posteroventral surface only weakly produced into blunt, chin-like protuberance, surface between protuberance and posterior margin appearing only slightly depressed in lateral view (Fig. 348); posterior margin slightly concave in ventral and dorsal views (Figs. 346, 347). Apex of each paramere narrowly rounded in medial view, apex bent dorsad (Fig. 339); narrowly rounded in ectal view (Fig. 341); roughened, spiculate area on lateral surface ovoid, localized (Fig. 340). Aedeagus with conjunctival lobes large, each lateral lobe with 2 obtuse diverticula (Fig. 344); median penial lobes and penisfilum relatively small, obscured by conjunctival lobes (Fig. 342); dorsomedial conjunctival lobe relatively large (Fig. 343).

Measurements. Total length 7.41–9.46 (7.41); total width 5.20–5.83 (5.20); medial length of pronotum 1.66–1.88 (1.66). Medial length of scutellum 3.39–3.90 (3.39); basal width 3.31–3.68 (3.31); width at distal end of frena 1.10–1.40 (1.10). Length



Figs. 337–351. *T. infuscata.* 337. Habitus. 338. Head. 339–341. Right paramere. 339. Medial view. 340. Lateral view. 341. Ectal view. 342–344. Theca and related structures. 342. Ventral view. 343. Dorsal view. 344. Lateral view. 345–348. Pygophore. 345. Caudal view. 346. Ventral view. 347. Dorsal view. 348. Lateral view. 349. Genital plates, caudoventral view. 350. Spermatheca. 351. Spermathecal pump.

of head 1.46–1.64 (1.46); width 2.08–2.21 (2.08). Length of segments 1–5 of antennae 0.39–0.44 (0.39), 0.77–0.88 (0.77), 1.03–1.10 (1.03), 1.10–1.29 (1.10), and 1.10–1.21 (1.10), respectively. Length of segments 2–4 of rostrum 1.23–1.29 (1.23), 0.74–0.77 (0.77), and 0.74–0.75 (0.75), respectively.

Holotype. ♂ labeled "ECUADOR: Pichincha Prov. Tinalandia; 12 km E Sto. Domingo de los Colorados. ca. 2,500 ft, 11–17-V-1986. J. E. Eger, coll." Deposited in the Florida State Collection of Arthropods (Gainesville).

Paratype. 1♀. Labeled same as holotype (♀ FSCA).

Distribution. Ecuador (Map 2).

Comments. No other species of *Thyanta* has the inner basal angle of each hemelytral membrane distinctly infuscated.

Etymology. Named for the infuscated basal angle of the hemelytral membrane.

Thyanta (Argosoma) straminea Rider, new species
Figs. 352–356, Map 2

Description. Dorsal surface pale green, head and anterior disc of pronotum yellowish-brown, exocorium stramineous, apex of scutellum and apex of each humeral angle reddish; punctures pale brown.

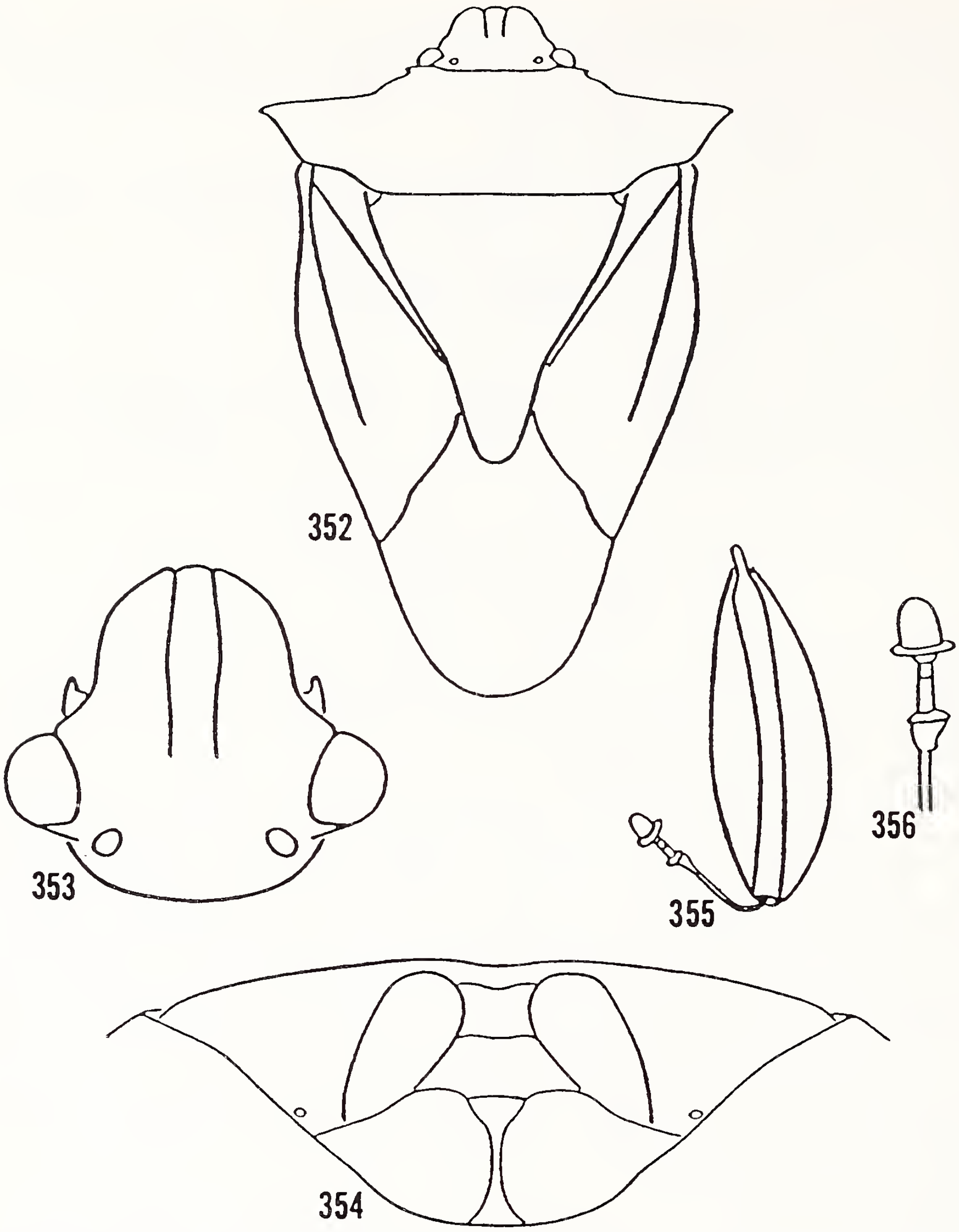
Apex of head evenly rounded; outer jugal margins not quite parallel (Fig. 353); surface transversely tumid, densely and evenly punctate. Anterolateral margins of pronotum in dorsal view concave; humeral angles acutely produced, nearly spinose, protruding beyond base of adjacent coria by more than width of eye (Fig. 352). Pronotal disc uniformly punctate except punctures somewhat crowded anterior to cicatrices; pronotal cicatrices immaculate. Hemelytra rather sparsely punctate especially on distal fourth; posterior margins nearly straight; costal angles acute, reaching to anterior margin of last connexival segments; hemelytral membranes hyaline with a few faint brown flecks distally. Connexiva not exposed, pale yellow, posterolateral angles of segments black.

Ventral surface stramineous with greenish hues on head and propleura; punctures concolorous with surface. Rostrum stramineous with brown markings, distal half of segment 4 piceous, reaching onto base of abdomen. Apex of humeral angles reddish. Ostiolar canals acuminate apically. Femora and tibiae stramineous, tarsal segments and apex of each tibia brownish. Postspiracular spots vague, green; posterolateral angles of abdominal sternites piceous.

Mesial margins of basal plates in caudoventral view convex, separated basally and distally; posterior margins sinuous; posteromesial angles brown, weakly emarginate (Fig. 354); surface of each basal plate punctate on mesial half. Distal end of sclerotized rod slightly swollen subapically, narrowed apically (Fig. 355); only small amount of swelling and coiling below proximal flange (Fig. 356). Male unknown.

Measurements. Total length 7.57–8.28 (8.28); total width 5.68–5.96 (5.96); medial length of pronotum 1.50–1.81 (1.81). Medial length of scutellum 3.46–3.64 (3.64); basal width 3.24–3.31 (3.31); width at distal end of frena 1.18–1.32 (1.32). Length of head 1.55–1.59 (1.59); width 1.99–2.08 (2.08). Length of segments 1–5 of antennae 0.40, 0.78–0.79 (0.78), 0.92–1.07 (1.07), 1.05–1.14 (1.14), and 1.10, respectively. Length of segments 2–4 of rostrum 1.23–1.29 (1.29), 0.70–0.75 (0.70), and 0.68–0.75 (0.75), respectively.

Holotype. ♀ labeled (a) "Buenaventura Colombia '44 C. L. Fagan" (b) "Thyanta



Figs. 352–356. *T. straminea.* 352. Habitus. 353. Head. 354. Genital plates, caudoventral view. 355. Spermatheca. 356. Spermathecal pump.

acutangula Jen-Har. det. H. Ruckes." Deposited in the American Museum of Natural History (New York).

Paratype. 1♀. "ECUADOR: Napo Province, Limoncocha, on Rio Napo 13-XI-1973 Boyce A. Drummond, III Blacklight Trap" (♀ USNM).

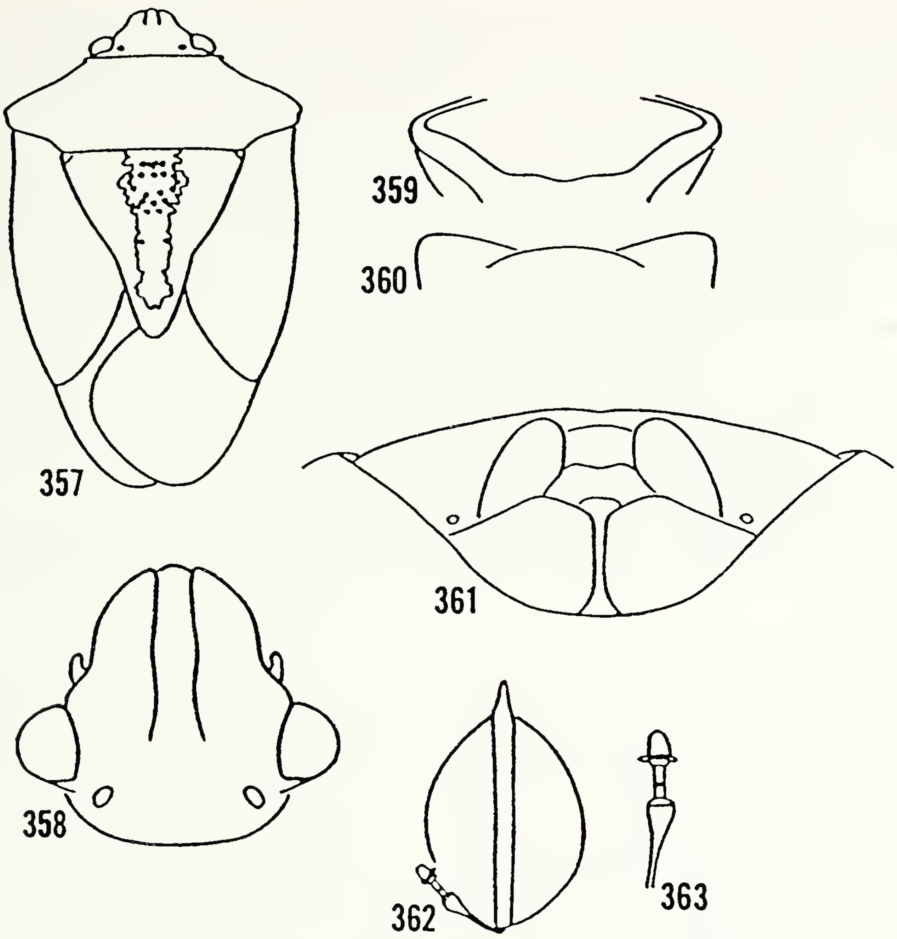
Distribution. Colombia and Ecuador (Map 2).

Comments. The acutely produced humeral angles and the stramineous-colored exocorium will easily identify this species within the subgenus *Argosoma.*

Etymology. Named for the stramineus-colored exocorium.

Thyanta (*Argosoma*) *similis* Van Duzee
Figs. 357–363

Thyanta similis Van Duzee, 1933:26–27; Barber, 1934:282; Linsley and Usinger, 1966:133; Froeschner, 1981:71; Froeschner, 1985:43–44.



Figs. 357–363. *T. similis.* 357. Habitus. 358. Head. 359–360. Pygophore. 359. Caudal view. 360. Ventral view. 361. Genital plates, caudoventral view. 362. Spermatheca. 363. Spermathecal pump.

Diagnosis. Small; ovate; distinctly convex. Green to testaceous often marked with dark rubescence on scutellum, hemelytra, and posterior disc of pronotum. Scutellum with medial longitudinal band from base to near apex nearly impunctate, subcalloused, cream-colored.

Apex of head broadly rounded; outer jugal margins subparallel for middle third of distance from eyes to apex (Fig. 358); dorsal surface of head evenly but distinctly convex transversely. Anterolateral margins of pronotum concave in dorsal view; humeral angles rounded (Fig. 357). Pronotal cicatrices immaculate. Ostiolar canals acuminate apically. Mesial margins of basal plates in caudoventral view straight to slightly convex; posterior margins sinuously convex; posteromesial angles truncated (Fig. 361). Distal end of sclerotized rod slightly swollen subapically, narrowed apically (Fig. 362); spermathecal duct slightly swollen below proximal flange (Fig. 363). Posterior margin of pygophore sinuously U-shaped in caudal view (Fig. 359); concave in lateral view. Apex of each paramere spinose in ectal view; narrowly rounded in medial view; dorsomedial concave surface oriented more dorsad than mediad; roughened spiculate area on lateral surface circular.

Types. Van Duzee (1933) described *T. similis* from 2♀♀ both collected in the Galapagos Islands. Both specimens were examined and are conserved in the California Academy of Sciences (San Francisco).

Distribution. Known only from the Galapagos Islands, Ecuador.

Specimens examined. Five specimens collected between 22 January and 24 April; deposited in CAS, DAR, SMEK. ECUADOR: GALAPAGOS ISLANDS: *Floreana Island:* Post Office Bay. *Rábida Island. Santa Cruz Island:* Academy Bay.

Comments. Thyanta similis and *T. setigera* are the only two species of *Thyanta* known to occur in the Galapagos Islands. These two species are easily separated by the shape of the humeral angles, which are rounded in *T. similis* and angulate to spinose in *T. setigera. Thyanta similis* is the only species in the genus that has the medial portion of the scutellum nearly impunctate and subcalloused.

Thyanta chilensis (Herrich-Schäffer), *nomen dubium*

Pentatoma chilense Herrich-Schäffer, 1853:323; Signoret, 1863:547.
Pentatoma chilensis: Walker, 1867:290; Reed, 1898:26.
Thyanta chilensis: Lethierry and Severin, 1893:148; Kirkaldy, 1909:94; Jensen-Haarup, 1928:185.

The type specimen of *Pentatoma chilense* is no longer in existence, and Herrich-Schäffer's (1853) original description is not adequate to identify this species. Both Signoret (1863) and Reed (1898) state that the characters given are not sufficient to determine if it is a true *Pentatoma.* Kirkaldy (1909) transferred this species to the genus *Thyanta,* but he put a question mark beside the name. In his introductory paragraph to the key to *Thyanta* species, Jensen-Haarup (1928) stated that the key included all known species of *Thyanta* except several "dubious" species, one of them *T. chilensis.*

Herrich-Schäffer's description of *P. chilensis* does not match any of the three species of *Thyanta* known to occur in Chile: *T. juvenca, T. rubicunda,* and *T. xerotica. Thyanta xerotica* is relatively uncommon and occurs only in the coastal desert areas of northern Chile to Ecuador. Approximately equal numbers of *T. juvenca* and *T. rubicunda* in museums have been identified as *T. chilensis.* Due to the inadequacy of the original description, the lack of type material, and the confusion surrounding the name, *T. chilensis* should be considered a *nomen dubium.*

Thyanta immemor Kirkaldy, *nomen dubium*

Pentatoma inconspicua Dallas, 1851:250.
Thyanta inconspicua: Lethierry and Severin, 1893:148.
Thyanta immemor Kirkaldy, 1909:94; Jensen-Haarup, 1928:187–188 (replacement name).

Dallas (1851) described *T. inconspicua* without giving a type locality. Kirkaldy (1909) transferred the species to *Thyanta,* and renamed it *T. immemor,* without commenting on either the name change or the transfer to *Thyanta.* Jensen-Haarup (1928), evidently unaware of the name change, included *T. inconspicua* in his key to species, but the couplet is essentially a repeat of Dallas' original description and no locality is given.

Although many of Dallas' type specimens still exist and are housed in the British Museum of Natural History, the type of *T. inconspicua* was not located. Dallas' original description is fairly detailed and contains several characters which would preclude this from being a species of *Thyanta.* Dallas described *T. inconspicua* as

having six lines of brown punctures on the head and a red spot on the ventral surface of the abdomen. These characters have not been observed in any specimen of *Thyanta*. This species may be valid, but it is doubtful that it belongs in *Thyanta*.

Thyanta humilis viridescens Kuhlgatz, *nomen dubium*

Thyanta humilis var. *viridescens* Kuhlgatz, 1903:256–257; Kirkaldy, 1909:94.

Kuhlgatz (1903) described *viridescens* as a variety of *T. humilis*. Although his description is fairly detailed for its time, this taxon cannot be identified with any certainty. The type specimens may have been destroyed during World War I or II. Kuhlgatz listed the distribution of *viridescens* as being from Panama to Guayaquil, Ecuador. The present study has placed *T. humilis* as a junior synonym of *T. patruelis*, which occurs from central Brazil and southern Peru to Argentina. So, it is unlikely that *viridescens* is a subspecies of *humilis* (=*patruelis*). *Thyanta humilis viridescens* should be considered a *nomen dubium*.

INCERTAE SEDIS

Thyanta vitrea (Westwood)

Pentatoma vitrea Westwood, 1837:36; Lethierry and Severin, 1893:199.
Thyanta vitrea: Distant, 1900a:812; Kirkaldy, 1909:95; Jensen-Haarup, 1928:13.

Westwood (1837) described *Pentatoma vitrea* from "Brasilia?." The description is very short and not adequate for accurate placement of this species. The type specimen, which is conserved in the Hope Entomological Collections, Oxford University, England, was examined. It lacks the abdomen, and its condition is too poor to properly place this species within *Thyanta*. In fact, it may actually be a species of the closely related genus *Cyptocephala*.

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TWO NEW NEOTROPICAL GENERA OF TREPOBATINAE (GERRIDAE: HETEROPTERA)

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Abstract.—Two new genera and one new species of Trepobatinae (Gerridae) are described from South America. The new genera are compared with other American genera of the subfamily Trepobatinae. The new taxa described are: *Telmatometroides* new genus, monobasic, from estuarine habitats in the eastern tropical Pacific region, type-species *Telmatometra rozeboomi* Drake and Harris 1937; *Cryptobatoides* new genus, monobasic, from small headwater streams near Manaus, Brazil, type-species *Cryptobatoides brunneus,* n. sp.

This is the first of several papers dealing with the subfamily Trepobatinae. The generic names proposed here are needed for other works in progress dealing with classification, faunistics and zoogeography. Much of the material reported here was collected during a recent expedition to South America.

Excluding the two new genera described here, the subfamily Trepobatinae presently contains 13 genera worldwide, 6 of these in the New World. In Table 1 selected salient characters of the American genera are compared, excluding *Metrobates* which stands quite apart from the other genera, possessing a distinctly dorsoventrally flattened body, modified second and third antennal segments, relatively long middle tibia, conspicuous middle and hind leg claws, and a distinct fore-tibial process (cf. Andersen, 1982, p. 237). The subfamily attains its greatest diversity in the tropics of the southern hemisphere, and provides an interesting study in vicariance biogeography. In material collected in Australia and the Malay Archipelago, five additional undescribed genera of the subfamily are recognized and will be treated in forthcoming publications, along with a review of the higher classification of the subfamily.

The disposition of material and types is indicated in the descriptions, and abbreviations for institutions are given in the acknowledgments section. All measurements are in millimeters.

Telmatometroides, new genus
Figs. 1–4

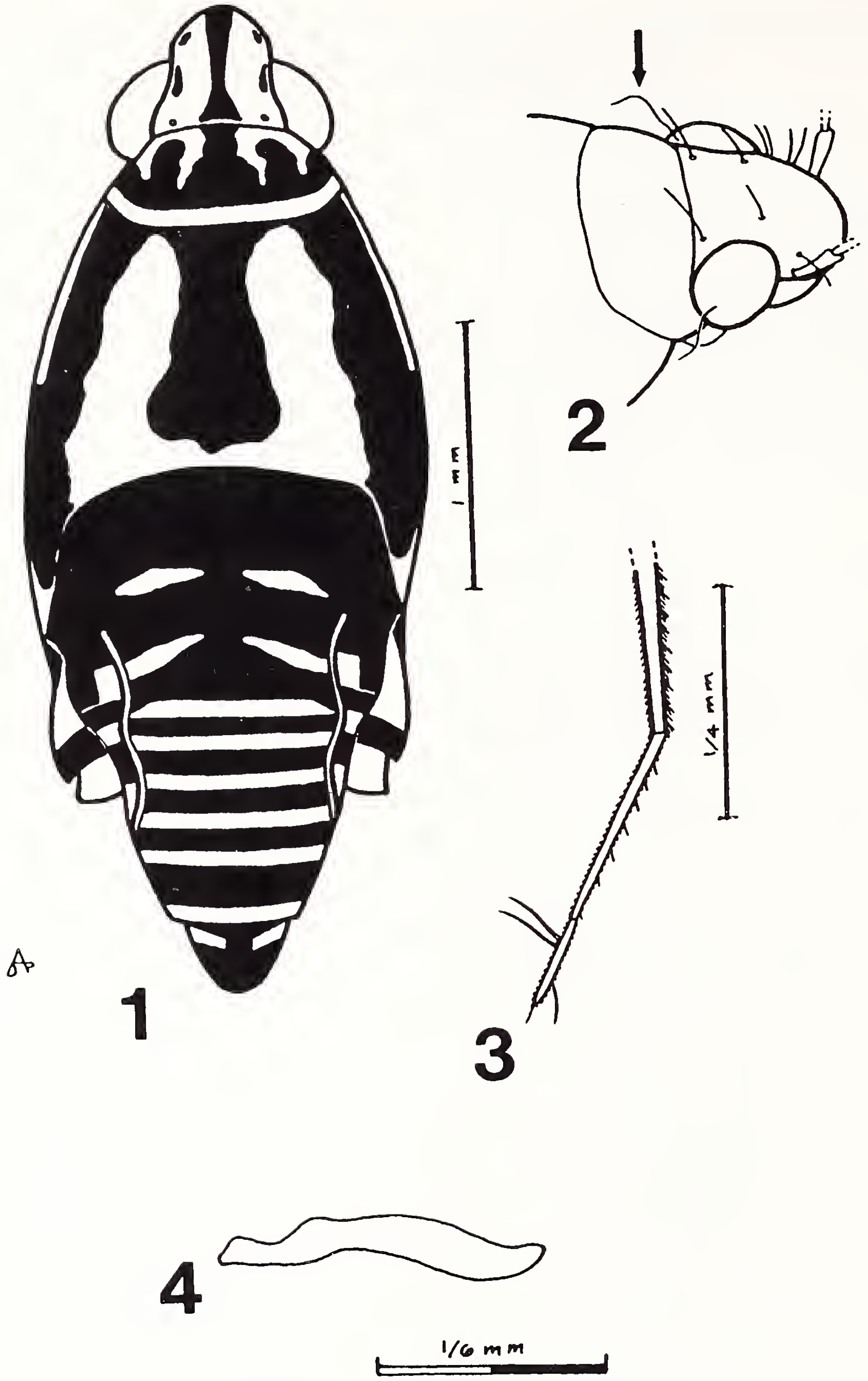
Diagnosis. Telmatometroides is separable from all closely related genera by the extensive black markings on the posterior part of the mesosternum, the row of 5 or 6 short stout black spines on the inner margin of the first segment of the posterior tarsi (Fig. 3), the depressed glabrous median longitudinal fascia on the mesonotum (Fig. 1), and by the lanceolate first gonapophysis (blunt in *Telmatometra*). Other characteristics separating it from *Telmatometra* and other Neotropical genera of Trepobatinae are given in Table 1 (the genus *Metrobates* is quite divergent from the other trepobatine genera and is not included in the table).

Description. (Based on only included species, *rozeboomi.*) Length of body, apterous males 2.8–3.6 mm; apterous females 3.4–3.7 mm; macropterous forms unknown.

Table 1. Generic characters—Neotropical Trepobatinae.

Character	Telm	Telt	Trep	Tret	Cryp	Ovat	Halt
Interocular space/eye width	1.0 to 1.1	1.4 to 1.7	1.3	1.3 to 1.4	1.6 to 1.9	1.4 to 1.6	1.1
Eye shape	elongate	elongate	globular	elongate	appressed	globular	globular
Dark median fascia on head	no	yes	yes	yes	no	yes	yes
Ratio, length, antennal segments III/II	2.2 to 2.4	1.4 to 1.5	1.1 to 1.2	1.2	1.7	1.2	1.4 to 1.5
Ratio, length, antennal segments III/I	1.2 to 1.4	1.1 to 1.2	0.7	0.4	1.1 to 1.2	0.7	0.8
Ratio, length, mid femur/ pro- + mesonotum	1.6 to 2.1	1.3 to 1.5	1.2 to 1.3	1.8 to 1.9	1.1 to 1.3	1.4 to 1.5	2.0
Ratio, length, hind tibia/tarsi	2.1 to 2.8	1.5 to 2.0	1.6	2.6 to 2.8	1.5 to 1.7	1.5	2.3 to 2.5
Male paramere	broad medially	slender, sinuate	falcate	slender, curved	slender, curved	slender, curved	falcate

Legend: Telm, *Telmatometra;* Telt, *Telmatometroides;* Trep, *Trepobates;* Tret, *Trepobatoides;* Cryp, *Cryptobatoides;* Ovat, *Ovatametra;* Halt, *Halobatopsis.*



Figs. 1–4. *Telmatometroides rozeboomi* (Drake and Harris). 1. Habitus, female. 2. Head, dorso-lateral view, showing long ocular setae (arrow). 3. Posterior tarsi. 4. Male paramere.

Ground color leucine to brownish yellow, heavily marked with black (see Fig. 1; also habitus figures in Drake and Harris, 1937 and Kenaga, 1941); black median stripe continuous from fore part of head nearly to posterior margin of mesonotum, interrupted briefly by the narrow posterior pronotal margin; this stripe not of even width, broader posteriorly both on pronotum and mesonotum; pronotum laterally ornamented with black fasciae; broad black stripes along mesopleura coalescing posteriorly; abdominal tergites extensively marked with black; black markings on the middle of the pronotum and mesonotum, and covering most of metanotum and

abdominal tergites II–VII with extensive shining areas; median black area of pronotum depressed. Venter leucine, with median longitudinal black stripe commencing at distal ⅔ of mesonotum, broadening posteriorly, continuous to posterior margin of abdominal sternite VII; this band in females crossed by a transverse black stripe on posterior edge of mesonotum and all of metanotum.

Structural characteristics. Head long, narrowly rounded anteriorly; eyes smaller than in *Telmatometra.* Width much less than interocular space (see Table 1), extending posteriorly along pronotum; ocular setae very long (Fig. 2; see Andersen, 1982, pp. 192–194 for discussion). Antennae long, slender; segment III about 1.5 times as long as II, slightly longer than I. Pronotum short, truncate posteriorly; length on midline of pronotum, 0.40; mesonotum, 0.83; metanotum, 0.47. Abdominal tergites I–VII subequal in length (0.14–0.18), except II longer (0.29). Male anterior femur slightly arched basally, flattened beneath, without spines or other modifications; anterior tibia slightly arched over entire length. Mesosternum without visible omphalium. Pregenital abdomen, genital segments without modifications. Parameres symmetrical, narrow (Fig. 4). Female gonapophysis 1 lanceolate.

Proportions of legs as follows:

	Femur	Tibia	Tarsal 1	Tarsal 2
Anterior	1.37	1.30	0.07	0.43
Middle	1.69	2.99	1.08	0.86
Posterior	2.20	1.15	0.18	0.54

Discussion: Telmatometra rozeboomi was described by Drake and Harris (1937: 358–360, fig. 2b) from a male and female from Panama, with no habitat data given. This taxon remained essentially unknown until recent collections because the type-series resides in the Drake Collection which is not readily available. When Kenaga (1941) revised the genus *Telmatometra* he did not see this species, however he noted that it did not fit his generic description. In Andersen's (1982:422) key to the Trepobatinae this taxon drops at couplet 10. It does not belong in *Telmatometra* or any of the genera that follow, not surprising now that the habitat is known to be marine; all of the closely related genera are known only from fresh water.

Type-species. Telmatometra rozeboomi Drake, C. J. and H. M. Harris 1937, new combination, monobasic.

Etymology. The generic name pertains to the superficial resemblance between this taxon and *Telmatometra.*

Distribution. COLOMBIA (Cauca; Chocó; Narino; Valle de Cauca); ECUADOR (Atacames); PANAMA (Bahia Honda, Pacific side).

Habitat/ecological notes. This species inhabits mangrove swamps in Panama and Colombia. In Colombia, specimens were collected in mangrove swamps having a wide salinity range and various mangrove species, e.g., *Rhizophora* spp., *Avicennia germinans, Laguncularia racemosa, Pelliciera rizophorae* and *Mora megitosperma.* It was collected in accompaniment with various other marine Gerromorphans (detailed in Polhemus and Manzano, in press). In a pond fed by fresh water streams but connected with the Bay of Buenaventura at high tide it was collected along with several freshwater Gerromorphans, e.g., *Brachymetra albinerva* Amyot and Serville, *Mesovelia zeteki* Harris and Drake.

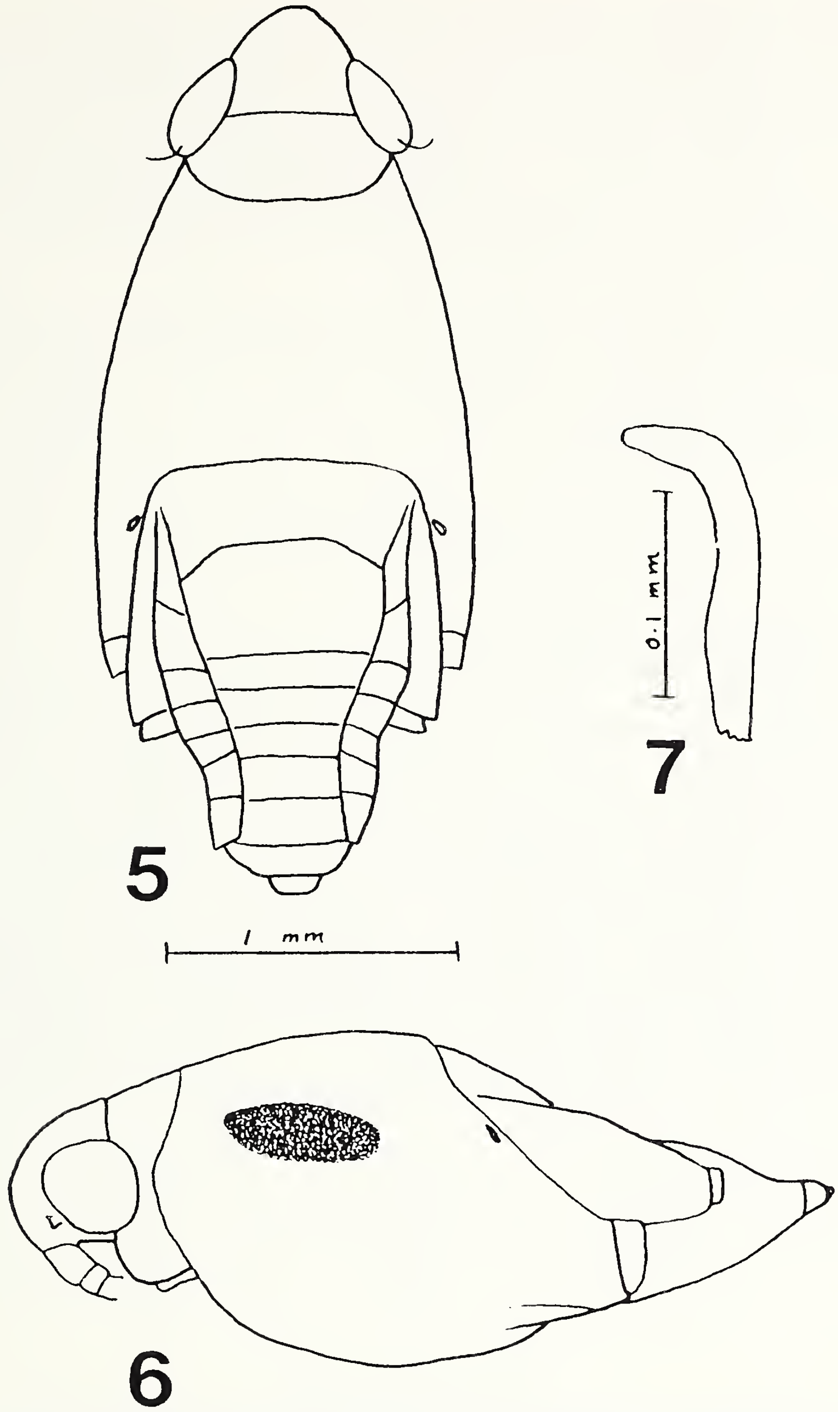
Cryptobatoides, new genus
Figs. 5–7

Diagnosis. Cryptobatoides is most closely related to the genera *Telmatometra* and *Ovatametra* (see Table 1). It differs from both genera in the soft brown ground color without contrasting markings (similar to some *Cryptobates* species), very elongate eye shape (in dorsal view), ratio of the antennal segments, extremely short legs, and by the unique oval lateral brown spot on the mesothoracic pleura of the male. The elongate appressed eyes immediately set *Cryptobatoides* apart from *Ovatametra* which has globular exserted eyes; in *Telmatometra* the eye shape is intermediate between these two genera. *Ovatametra* shares the short legs, but the middle femur is at least 1¼ times as long as the combined midline length of the pronotum and mesonotum, whereas in *Cryptobatoides* it is only slightly longer. In *Cryptobatoides* the third antennal segment is about half again as long as the second, whereas in *Ovatametra* the reverse is true; in *Telmatometra* the third segment is more than 2 times as long as the second.

Description. (Based on the only included species, *C. brunneus,* n. sp.) Apterous form: Length of body, males 2.6–3.0 mm, females 2.9–3.2 mm. Ground color mat yellowish brown to orange brown with brown to blackish brown markings, without pruinose markings. Entire dorsum densely set with very short dark appressed setae. Head laterally weakly embrowned along eyes, otherwise without markings. Pronotum infused with orange posteriorly. Mesonotum of male with an elongate triangular brownish marking anteriorly, posteriorly with a longitudinal dark brown median stripe continuing posteriorly onto abdominal tergite 2, these median markings less pronounced in females; both males and females with a brown sinuate band laterally, males in addition with a sharply defined elongate oval dark brown spot on the upper pleural region (Fig. 6). Dorsum with additional dark markings on metanotum and abdominal tergite 1, connexiva and abdominal tergites very narrowly margined with brown; pleural region broadly brownish. Venter completely luteous except mesoacetabular cleft darkened anteriorly. Legs, antennae brown to dark brown, basally lighter, mid and posterior acetabulae margined with dark brown; coxae, trochanters at least ventrally yellowish.

Structural characteristics. Head long, rounded anteriorly, ventrally flattened; sides rounded along inner eye margins, anteclypeus not prominent; interocular space less than 1½ times eye width; eyes not exserted, elongate, extending posteriorly almost to mesonotum, ocular setae short (Fig. 5); rostrum slender, long, straight, extending almost to middle of mesosternum, with 4 very prominent segments, second shortest and ring-like, third very long, one and four subequal. Antennae moderately long, relatively slender, not sexually dimorphic; segments I and IV of equal length, substantially longer than II and shorter than III. Pronotum short, anterior and posterior margins almost straight, length on midline about ¼ that of mesonotum; width less than head through eyes. Mesonotum long, sides weakly convex, widening posteriorly, anteriorly almost straight and contiguous with pronotal margins, slightly narrower than head. Metanotum indicated by a weak suture laterally, evanescent medially, fused with abdominal tergites 1 and 2. Abdominal tergites 3–6 subequal in length, 7 longer.

Male anterior femur cylindrical, not thickened; tibia weakly broadened and flat-



Figs. 5–7. *Cryptobatoides brunneus,* n. gen., n. sp. 5. Habitus, female. 6. Side view, male. 7. Male paramere.

tened distally, almost as long as fore femur, without apical spur, inner face clothed with short stiff setae; anterior tarsal segment 1 short and cylindrical, segment 2 flattened distally, length of entire tarsus about ⅓ that of fore tibia. Middle femur thickened, much stouter and shorter than mid tibia or hind femur; tarsi long, first segment subequal to length of second. Hind femur relatively short, slightly thickened, about 1.5× as long as hind tibia; tarsi short, segment 1 slightly longer than 2. Claws of fore leg short, narrow, blade-like, almost straight, situated at middle of second tarsal segment, downcurving arolia flattened, as long as claws, dorsal arolia not evident; of middle leg long, very slender, curved, arising near middle of second tarsal

segment, extending to tip of tarsus, arolia not evident, but with a tiny stiff setae extending distally from apex, in addition to the normal long dorsal preapical curved setae; of hind leg preapical, reduced, slender, curved, arolia not evident. Female legs similar to male; middle and posterior legs of both sexes except distal tarsal segments set with short stiff spine-like setae. Pregenital abdomen, genital segments without modifications. Parameres symmetrical, narrow, bent distally (Fig. 7). Female gonapophysis 1 blunt and membranous distally.

Type-species. Cryptobatoides brunneus, n. sp., monobasic.

Etymology. The generic name *Cryptobatoides* refers to the superficial resemblance with some species of the genus *Cryptobates.*

Distribution. Brazil (Amazonas).

Cryptobatoides brunneus, new species
Figs. 5–7

Diagnosis. See generic description.

Description. Length, apterous male 2.87 mm (mean, N = 4; min. 2.63, max. 3.03); apterous female 3.04 mm (mean, N = 10; min. 2.93, max. 3.18). Width, apterous male 1.21 mm (mean, N = 4; min. 1.16, max. 1.26); apterous female 1.35 mm (mean, N = 10; min. 1.26, max. 1.41). Coloration; see generic description.

Structural characteristics. Apterous male (see generic description; only additional details given here). Head length 0.30, width 0.70; eye width (0.20), ⅔ of interocular space (0.30). Pronotum short, length 0.23, width 0.60; mesonotum long, broad, sides weakly convex, length 0.83, width 0.98; metanotum length 0.30, width 0.60, fused with first two abdominal tergites, all well indicated except medially, tergite 1 length 0.15, tergite 2 length 0.18; abdominal tergites III–VI equal in length (0.10), 7 longer (0.13). Length of antennal segments I–IV, 0.45: 0.35: 0.55: 0.45.

	Femur	Tibia	Tarsal 1	Tarsal 2
Anterior	0.75	0.70	0.05	0.20
Middle	1.18	2.00	0.68	0.75
Posterior	1.38	0.85	0.33	0.25

Abdominal terminalia not modified; paramere as shown in Figure 7.

Apterous female. (See generic description; only additional details given here.) Structure and coloration mostly as in male, except slightly larger and more robust; antennae and legs similar to male; abdominal tergite VIII directed slightly ventrad, broadly notched posteriorly, embracing proctiger.

Macropterous male. Length of body 2.78 mm, to tip of wings 3.79 mm, width 1.16 mm. Similar to apterous male in coloration and other structures except the longer (1.21) and wider (1.01) pronotum. Fore wing dusky gray brown, with two closed cells basally, a transverse line of weakness at basal ⅓, very similar to that of *Trepobates taylori* (Kirkaldy) (see Andersen, 1982:215, fig. 428). Hind wing infuscated, with one closed cell basally, the cross vein at basal ¼, similar to the trepobatine wing illustrated by Andersen (loc. cit., fig. 429) except the cross vein is more basally located.

Macropterous female. Length of body 3.08–3.18 mm (all specimens dealated), width 1.26–1.31 mm. Similar to macropterous male in structures and coloration. The pronotum is translucent posteriorly revealing the dark wing bases folded beneath,

which gives the appearance of a posterior dark band, particularly in alcohol specimens. Pronotum longer (1.26) and wider (1.11) than apterous form.

Discussion. This species vaguely resembles the smaller *Telmatometra* species, but lacks the contrasting markings of those taxa. In general facies it more closely resembles *Cryptobates obscurus* Miyamoto from Borneo.

Etymology. The name *brunneus* refers to the soft brown coloration without prominent markings.

Habitat data. This species was collected only in small streams (Igarapés) in the seasonally dry rain forest near Manaus. These water striders are not strong skaters, thus they are found only in still pools in the forest or along the sides of streams. On one occasion at the type locality, a specimen was observed producing concentric ripples on the surface of the water, apparently communicating with congeners in a manner described by Wilcox (1972) for *Rhagadotarsus* species (Polhemus 1990).

Holotype. Apterous male: BRAZIL, Amazonas: Small blackwater stream in primary rain forest at INPA Forest Management Station, 98 km NW of Manaus, 90 m, water temp. 25°C, VIII-29-89, CL 2477, J. T. and D. A. Polhemus (INPA).

Paratypes (all apterous unless otherwise noted; all collected by J. T. and D. A. Polhemus, and R. T. de M. Sampaio). BRAZIL, Amazonas: 30 males, 2 macropterous male (dealated), 30 females, 11 nymphs, same data as type; 9 apterous males, 1 macropterous male, 7 apterous females, 2 macropterous females (dealated), small blackwater trib. to Rio Cuieras, Reserva Biologia de Campina, off Hwy. 174 at km 62, N of Manaus, 100 m, water temp. 23.5°C, pH 3.2, VIII-23-89, CL 2468; 43 males, 1 macropterous male (dealated), 43 females, 29 nymphs, Igarapé de Anta, 2.5 km E of INPA Reserva Ducke HQ, 25 km NE of Manaus, 60 m, water temp. 24.5°C, VIII-25-89, CL 2472; 29 males, 37 females, 7 nymphs, Igarapé Barro Branco, at INPA Reserva Ducke HQ, 50 m, water temp. 23.5°C, pH 5.6, VIII-27-89, CL 2475; 8 males, 10 females, 8 nymphs, small clear rainforest stream near INPA A. Egler Reserve, 70 m, water temp. 24.5°C, VIII-30-89, CL 2479; 2 males, 1 macropterous male (dealated), 1 female, 1 nymph, small stream in primary rainforest near INPA viewing tower along road to INPA Forest Management Station, 90 m, VIII-29-89, CL 2478 (JTPC, ZMUC, INPA).

ACKNOWLEDGMENTS

My special thanks go to Dan A. Polhemus for invaluable assistance in the field, inking Figures 1–4, and reviewing the manuscript. I wish to thank the following people who helped make our field work successful in South America: Raquel Telles de Moreira Sampaio and Victor Py-Daniel, INPA, Manaus, Brazil; Maria del Rosario Manzano, Universidad del Valle, Cali, Colombia. The type of *Cryptobatoides brunneus* is deposited in the Instituto Nacional de Pesquisas de Amazônia, Manaus (INPA); paratypes are in the J. T. Polhemus Collection, Englewood, Colorado (JTPC), the Zoological Museum, University of Copenhagen (ZMUC) and INPA; material of *Trepobatoides rozeboomi* (Drake & Harris) is in JTPC and the Universidad del Valle, Cali. This research was supported in part by a grant from the National Geographic Society, Washington, D.C., to whom I am deeply grateful for their continued support.

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A NEW COLEOPTEROID LETHAEINE FROM SOUTHERN SOUTH AMERICA (HEMIPTERA: LYGAEIDAE: RHYPAROCHROMINAE)

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Abstract.—*Stictolethaeus slateri,* new genus, n. sp., is described from Argentina and Uruguay. A new type of sexual dimorphism suggests male pheromone production. Coleopteroid forewings and the lack of hind wings apparently preclude flight.

The monotypic genus described below was discovered in the course of revisionary work on Western Hemisphere Lethaeini (Hemiptera: Lygaeidae: Rhyparochrominae) (O'Donnell, 1986). It exhibits several distinctive morphological features, including a highly modified forewing, unique genitalia, and unusual sexual dimorphism. Although this interesting new bug is clearly a member of the Lethaeini, the tribal concept must be broadened to include it.

MATERIALS AND METHODS

Specimens were borrowed from the institutions or personal collections listed in the Acknowledgments. Names of colors follow Smithe (1975). Standard procedures for dissection of genitalia and measurement of specimens were used. All measurements are in mm. Measurements of a paratype female (on the same pin as the holotype) are given in parentheses following those of the holotype in the species description. Locality data, etc. are given exactly as they appear on the labels.

For scanning electron microscopy, specimens were soaked overnight in relaxing fluid, dissected, and allowed to air-dry for several hours. They were then mounted on an aluminum stub with conductive wax, sputter-coated with gold for 4.5 minutes in a Polaron® sputter-coater, and examined with a Coates and Welter® Field Emission Scanning Electron Microscope. Photographs were taken at approximately 20 kv accelerating voltage, with a Polaroid camera at f6 for 16 seconds, using Polaroid PolaPlan 4 × 5 Land Film Type 52® processed according to manufacturer's directions.

Stictolethaeus, new genus

Description. Body broadly oval. Dorsal surface very finely rugulose, conspicuously punctate. Head with 2 basal iridescent areas composed of ridges 2 μm apart (Figs. 2, 4). Hemelytron coleopteroid, with no trace of membrane. Hind wing lacking. Fore femur lacking short, stout, distal spines beneath. Dorsal margin of metathoracic scent gland evaporative area with a deep notch (Fig. 3). Dorsum of abdomen sexually dimorphic (Figs. 6–9). Terminal abdominal terga of female fused, with tergum 8 entire (Fig. 16). Clasper (Fig. 13) conventional. Sperm reservoir (Fig. 14) unique.

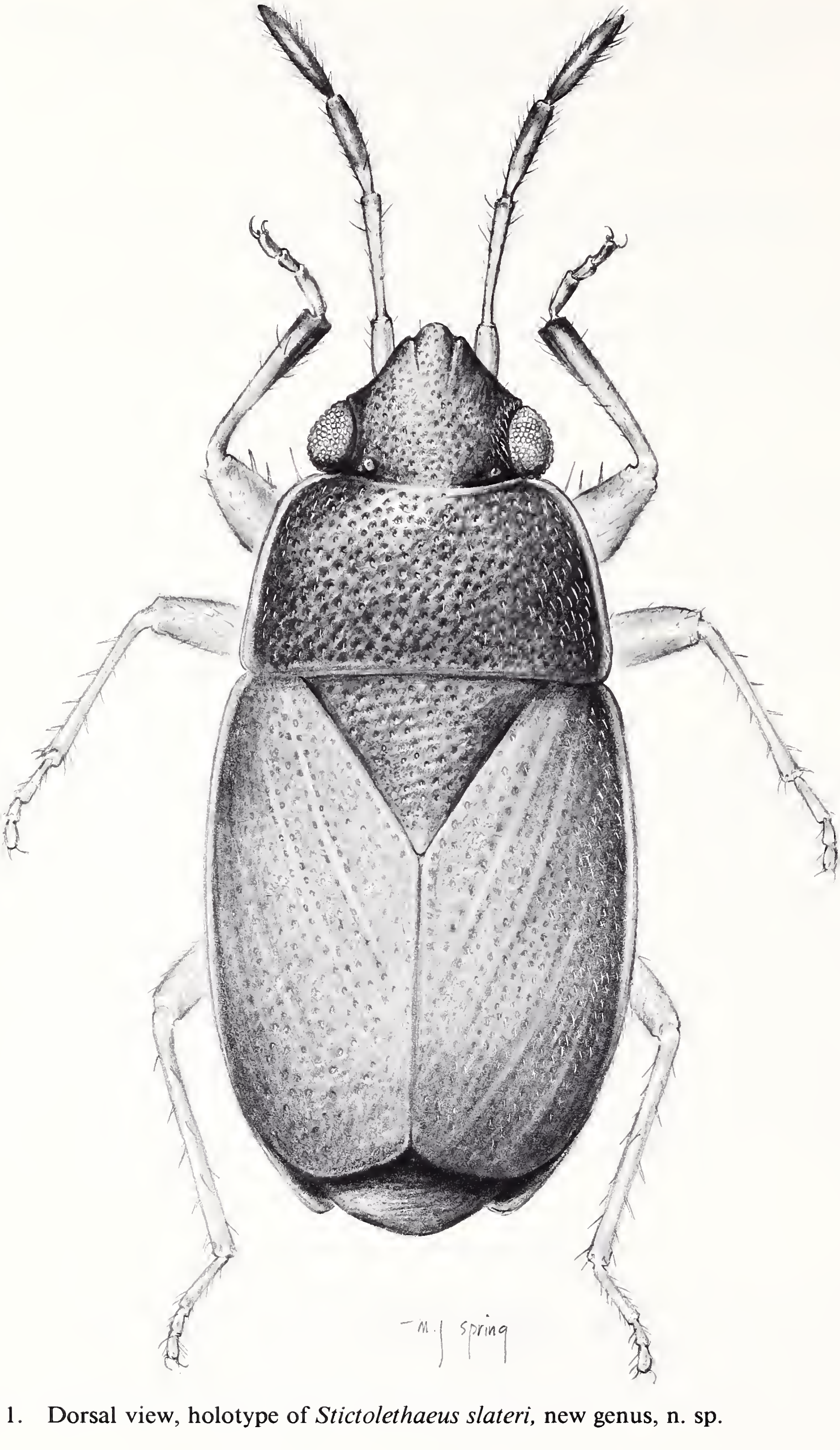


Fig. 1. Dorsal view, holotype of *Stictolethaeus slateri,* new genus, n. sp.

Spermatheca (Fig. 15) with only proximal flange apparent, and an asymmetrical sclerite between bulb and flange. Nymph with canals of scent glands 3–4 and 4–5 converging just laterad of gland openings, then diverging again (Fig. 10); tergum 4 of nymph reduced and partially fused with tergum 5 (Fig. 10).

Type species. Stictolethaeus slateri, n. sp.

Etymology. This genus takes its name from the Latin *sticto-*, meaning punctate, in reference to its heavily punctate dorsal surface, in combination with *Lethaeus,* for the type genus of the tribe.

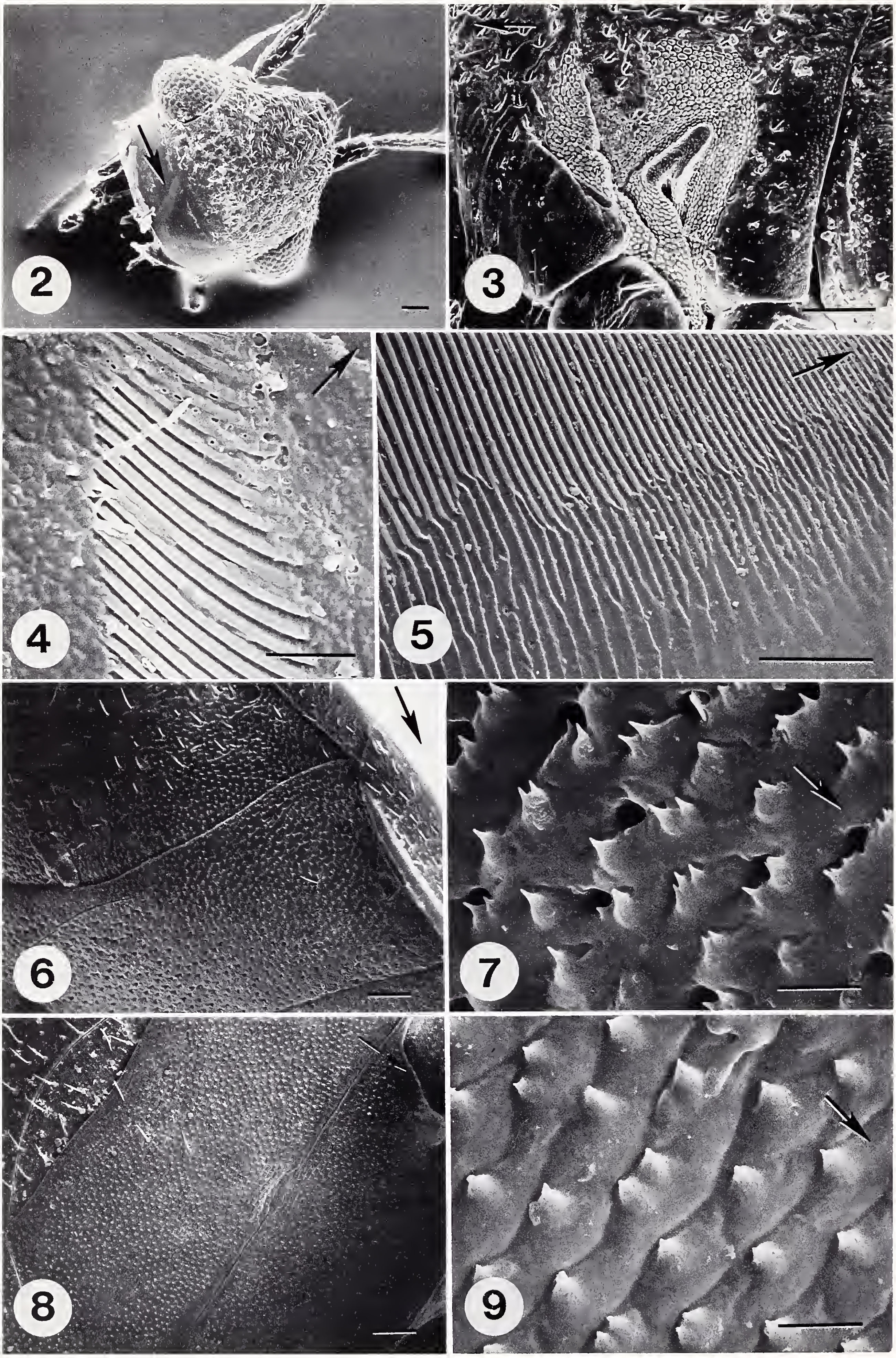
Stictolethaeus slateri, new species

Description. Small, total length 2.70 (3.30); broadly oval, maximum width 1.30 (1.53). Subshining, with a very fine, hexagonal rugosity overall. Dorsum entirely and evenly punctate, with short decumbent hairs (Fig. 1).

Coloration: Dorsal and ventral surfaces uniformly cinnamon-rufous, except for buff-yellow lateral pronotal and corial margins. Legs, first two antennal segments and proximal ⅓ of third antennal segment dark buff-yellow. Distal ⅔ of third segment and all of fourth contrastingly tawny. Extreme distal end of second antennal segment geranium red; exposed areas of terminal abdominal connexiva also tinged with geranium red.

Head: Vertex moderately swollen, with two rigid irridescent spots (Figs. 2, 4); ocelli present; jugum concave. Length head 0.48 (0.52); preocular length 0.25 (0.28); width head 0.72 (0.82); interocular width 0.42 (0.40). First antennal segment barely exceeding tylus, armed with stout hairs along inner surface; second antennal segment terete; third and fourth fusiform; distal half of second segment and all of third and fourth segments with upstanding hairs, longer than the diameter of segment, in addition to decumbent pubescence. Antenniferous tubercles unmodified. Length antennal segment I 0.22 (0.25); II 0.35 (0.40); III 0.28 (0.32); IV 0.40 (0.42). Venter of head very slightly swollen. Labium barely reaching mesocoxae, first segment not reaching base of head. Length labial segment I 0.35 (0.38); II 0.30 (0.35); III 0.22 (0.28); IV 0.25 (0.28).

Thorax: Pronotum with anterior and posterior margins shallowly concave; lateral margins explanate, only very slightly sinuate. Trichobothria level with anterior pronotal margin at meson. Pronotum not distinctly divided into anterior and posterior lobes. No collar, transverse impression or longitudinal furrow. Humeri not prominent or raised. Length pronotum 0.55 (0.60); posterior width 1.08 (1.25); width across trichobothria 0.75 (0.92). Scutellum broad, flat. Length 0.52 (0.60); width 0.70 (0.82). Hemelytron coleopteroid, truncate, covering all but terga 7 and 8 dorsally. Corial fracture laterad of R + M, extending ⅚ length of corium. Length corium along midline 0.85 (1.00). Legs short, stubby; fore femur most strongly swollen, armed below with a row of long hair-spines proximally, but no short, stout spines distally. Mid and hind femora armed below with a row of spines not quite as long as tibial spines. Fore tibia with reduced number of spines; mid and hind tibiae spinose. Metathoracic scent gland (Fig. 3) with ostiolar peritreme raised and sharply angled posteriorly. Evaporative area covering all of mesepimeron, extending dorsally along meso-metapleural junction to same level as evaporative area on metapleuron. Evaporative area covering ventral ⅘ of metapleuron; dorsal margin with broad notch anteriorly, almost reaching peritreme; postero-dorsal corner sharply curved.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Abdomen: 4–5 sternal suture not reaching 3–4 sternal suture. Spiracle 5 almost directly above middle trichobothrium of segment 5. (From paratypes) innerlaterotergites absent; scent gland scars between terga 3–4 and 4–5 converging and then separating again. Tergum 4 consequently very reduced, partially fused with tergum 5. Anterior abdominal terga of female almost entirely desclerotized (Fig. 16); cuticle of terga 6 and 7 modified, with flat, triangular, posteriorly-directed projections (Figs. 8, 9). Corresponding area of male abdomen typically sclerotized but perforated by numerous pores (Figs. 6, 7). Female with eighth tergum entire, uniquely shaped (Fig. 16). Male genitalia: clasper with broad, thumb-like inner projection (Fig. 13); sperm reservoir (Fig. 14) complex, shape unique for the tribe, with vesical seminal duct tightly coiled within sclerotized cylinder of vesica. Female genitalia: spermatheca (Fig. 15) with spherical bulb; proximal flange only present; assymmetrical sclerite present between bulb and flange.

Holotype. ♂ ARGENTINA, Pcla. Bs. As., Tandil, III-1963; Collection Dr. Carpintero, Argentina. Deposited in AMNH.

Paratypes (101♂♂, 134 ♀♀). ARGENTINA: 1♀, carded separately but on same pin as holotype; 1♂, 1♀ same data as holotype (carded separately, on same pin); 2♂♂, PBA Puntalara, XII-73; 1♂, Pcla. Bs. As., Otamendi, XI-1964; 2♂♂, Córdoba, Arias, VIII-1966, (carded separately, on same pin); 1♂, 1♀, Isla Tinbo (?) Santa Fe, XI-1971, (carded separately, on same pin); 1♂, Córdoba, V. Hermosa, III-1965, (carded separately, on same pin as a nymph, which is not a paratype); 1♂, Pcla. Bs. As., P. Iraola, II-1970, (carded); 1♂, 2♀♀ same data, (carded separately, on same pin); 2♂♂, same except II-1976, (carded separately, on same pin). All of the above specimens also bear an additional label: Coleccion Dr. Carpintero, Argentina. URUGUAY: 3♂♂, 10♀♀, Montevideo, VI-30-1967, Collectors L. and C. W. O'Brien; 1♀, Catamarca, El Suncho, II-1937, R. Goldbach; 19♂♂, 20♀♀, 1?, Montevideo, FDR Parque, 19 Sept. 1981, U-11, M.H. Sweet and P. Wilkinson; 3♂♂, 2♀♀, Montevideo, Beach W side of FDR Parque, 12 Oct 1981, U-17, M. H. Sweet and T. Stephens; 2♂♂ same except U-17B; 1♂, 3♀♀, Montevideo, FDR Parque, U-8B, 22 Nov 1981, M. H. Sweet; 1♂, 3♀♀, Montevideo, FDR Parque, U-5, 15 Sept 1981, M. H. Sweet and P. Wilkinson; 6♂♂, 5♀♀, Montevideo, near Airport, U-14, 10 Oct 1981, M. H. Sweet; 19♂♂, 36♀♀, Montevideo, FDR Parque, U-6, 16–19 Sept 1981, M. H. Sweet, T. Stephens and P. Wilkinson; 22♂♂, 23♀♀, Montevideo, FDR Parque, U-8, 18 & 20 Sept 1981, M. H.

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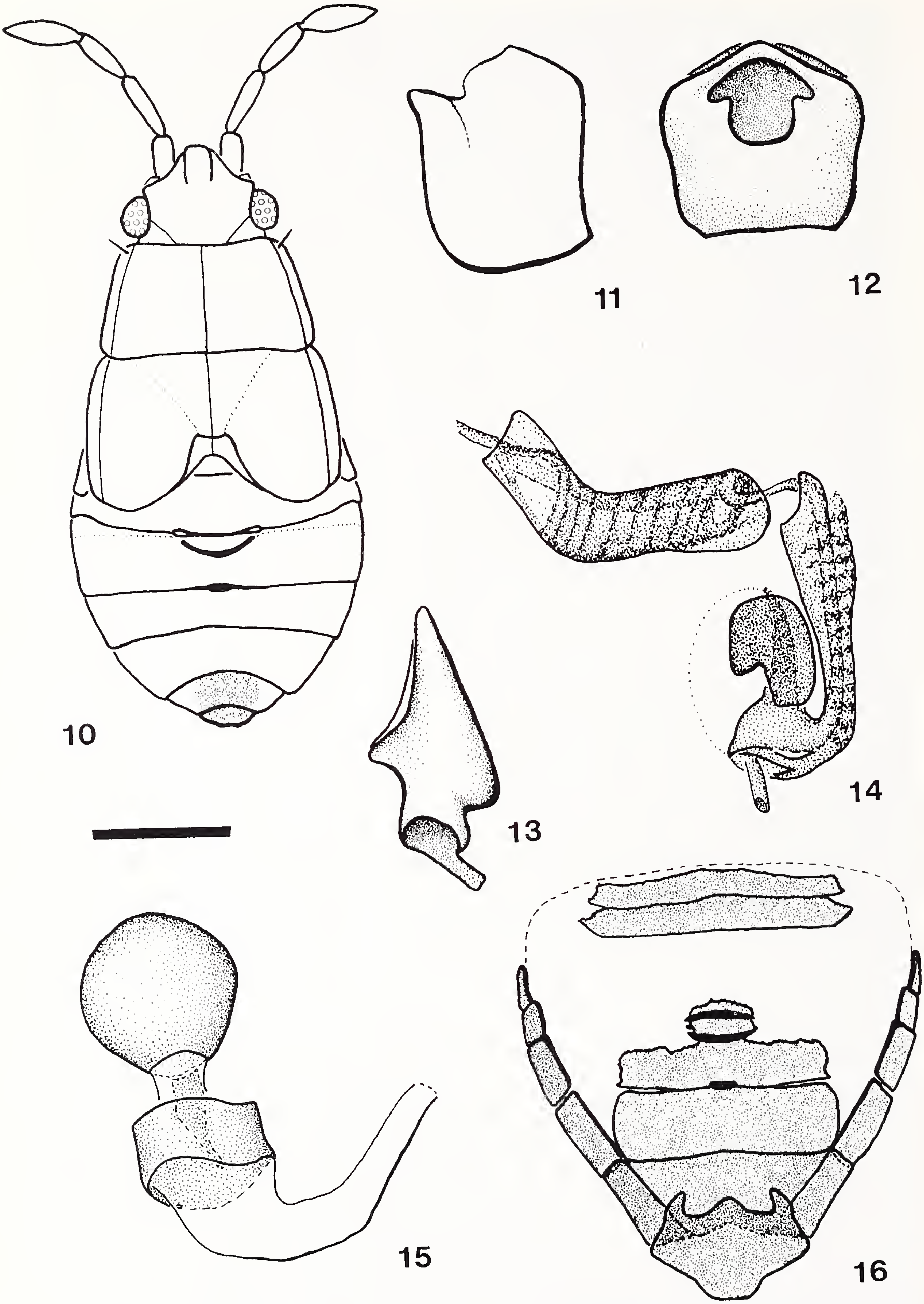
Figs. 2–9. Scanning electron micrographs. 2. Head of *Stictolethaeus slateri,* dorsal view, low magnification, with arrow showing iridescent spot. Scale bar = 50 μm. 3. *Stictolethaeus slateri,* metathoracic scent gland and surrounding evaporative area. Scale bar = 50 μm. 4. *Stictolethaeus slateri,* dorsal view of head, close-up of iridescent spot. Scale bar = 10 μm. 5. *Bubaces* sp., dorsal view of head, close-up of iridescent spot. Scale bar = 20 μm. 6. *Stictolethaeus slateri,* abdomen of male, dorsal view, low magnification. Arrow indicates anterior. Scale bar = 20 μm. 7. Same: fifth abdominal tergite of male, dorsal view, high magnification. Arrow indicates anterior. Note presence of pores (one at arrow). Scale bar = 10 μm. 8. *Stictolethaeus slateri,* abdomen of female, dorsal view, low magnification. Arrow indicates anterior. Scale bar = 20 μm. 9. Same, fifth abdominal tergite of female, dorsal view, high magnification. Arrow indicates anterior. Note absence of pores. Scale bar = 10 μm.



Figs. 10–16. *Stictolethaeus slateri*. 10. Fifth instar nymph, dorsal view. Scale bar = 0.5 mm. 11. Genital capsule, lateral view. Scale bar = 0.25 mm. 12. Genital capsule, dorsal view. Scale

Sweet, T. Stephens and P. Wilkinson; 1♀, Montevideo, FDR Parque, U-21, 28–29 Sept 1981, M. H. Sweet and T. Stephens; 1♀, Piriapolis, Cerro del Torro, 5 Oct 1981, U-23, M. H. Sweet, T. Stephens and P. Wilkinson; 2♂♂, 6♀♀, same except U-24; 8♂♂, 14♀♀, same except U-25; 1♂, 1♀, (blank) miles W of Rocha, 14 Oct 1981, U-27, M. H. Sweet; 1♀, FDR Parque, 28 Nov 1981, M. H. Sweet; 2♂♂, 2♀♀, 30 km N of Paysandu, Rio Queguay, U-32/33, M. H. Sweet. Deposited in CARP, AMNH, SWEET, JAS, and author's collections.

Etymology. Named for Dr. James A. Slater in recognition of his outstanding contributions to hemipterology.

Distribution. Argentina and Uruguay (Fig. 17).

Description of fifth instar nymph (pointed; Temperley, Argentina, Apr. 1906, R. Thaxter, AMNH) (Fig. 10): Head, pronotum, and wingpads (except laterally) chestnut. Lateral pronotal and wing pad margins buff yellow. Antennal segments I, II, and proximal two-thirds of III buff yellow. Distal end of segment III and all of segment IV cinnamon-rufous. Abdomen ground color ferruginous, marked with buff yellow as follows: lateral stripe; sublateral stripe; broken stripe just mesad of sublateral stripe; and series of dots, one per segment, midway between meson and lateral margin. Area immediately surrounding scent glands, and sclerotized plates on terga 8 and 9 cinnamon-rufous. Venter of thorax uniformly chestnut except for light buff yellow margins of meso- and metapleura. Venter of abdomen same color as dorsum. Legs cinnamon-rufous to cinnamon. Head broad, flat across vertex; with 2 basal iridescent spots composed of ridges (as in adult); jugum concave. Length head 0.42; width 0.65; interocular width 0.40. Antennal segment I fusiform, not exceeding tylus; segments II and III cylindrical, IV terete; segments II–IV covered with long upstanding hairs. Length antennal segments I 0.175; II 0.300; III 0.250; IV 0.375. Labium reaching mesocoxae. Length labial segments I 0.300; II 0.250; III 0.225; IV 0.250. Thorax: pronotum with trichobothrium at anterolateral corner; lateral margins explanate. Length pronotum 0.475; width across trichobothia 0.675; posterior width pronotum 0.925. Mesothoracic wing pad with explanate lateral margins; length mesothoracic wing pad 0.675. Abdomen with dorsal scent gland openings between abdominal terga 3–4 and 4–5 close together, with scent canals converging and nearly meeting just laterad of 3–4 scent gland opening, then diverging again; tergum 4 consequently very reduced between them (Fig. 10). Each scent gland opening surrounded by a narrow sclerite. Terga 8 and 9 with broad sclerotized plates; sterna 6 through 9 with broad mesal sclerotized plates. Length abdomen 1.10. Total body length 2.30.

Two additional nymphs were examined, each pointed on the same pin as a paratype (1 from Isla Tinbo, Santa Fe, Argentina and 1 from V. Hermosa, Cordoba, Argentina).

DISCUSSION

The placement of *Stictolethaeus* in the Lethaeini is unequivocal, since it exhibits the following characteristic tribal features (Ashlock, 1964; Slater and O'Donnell,

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bar = 0.25 mm. 13. Clasper. Scale bar = 0.1 mm. 14. Sperm reservoir, lateral view. Scale bar = 0.1 mm. 15. Spermatheca. Scale bar = 0.1 mm. 16. Abdomen of female, ventral view of tergites. Scale bar = 0.25 mm.

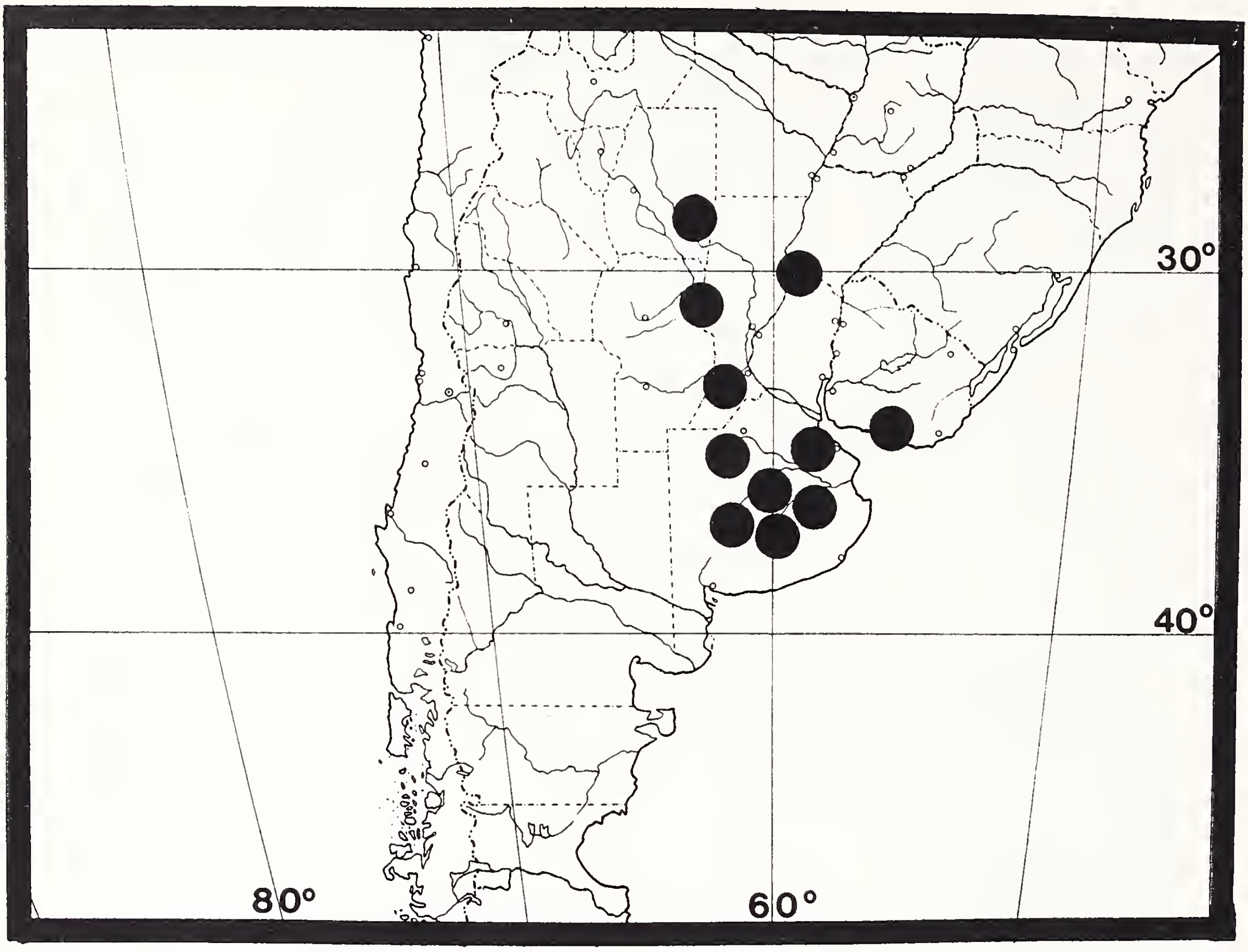

Fig. 17. Distribution of *Stictolethaeus slateri.*

1978): a rounded buccular groove joined immediately behind the labium; carinate juga; trichobothria at anterior corners of the pronotum; immatures with a reduced scent gland between abdominal terga 5 and 6; dorsum of head with iridescent areas basally; and generalized lethaeine male genital capsule and clasper.

The tribal definition must be modified, however, to include character states not usually found in the Lethaeini. Other members of the tribe have linear trichobothria on abdominal sternum 5, typically arranged with the anterior two trichobothria close together and widely separated from the third. In *Stictolethaeus slateri,* the 3 trichobothria are also linear, but almost evenly spaced. Curiously, the nymph of *Stictolethaeus slateri* has the typical lethaeine condition, possibly indicating that evenly spaced linear trichobothria are derived relative to other linear trichobothrial arrangements.

Stictolethaeus, unlike other lethaeines, does not have innerlaterotergites (Fig. 16). In their cladistic analysis of the tribes of Rhyparochrominae, Slater and Woodward (1982) did not include *Lilliputocoris* in the Lethaeini because it lacks innerlaterotergites, and erected a new, monotypic tribe for it for this reason. The loss of these structures in *Stictolethaeus* and *Lilliputocoris* may be convergent due to wing modification and accompanying changes in abdominal morphology; however, because there is a synapopmorphy uniting the tribes, the tribal placement of *Lilliputocoris* should be reexamined carefully.

The affinities of *Stictolethaeus* within the Lethaeini remain enigmatic. Most Neo-

tropical lethaeines belong to a clade defined by the possession of a single dorsal iridescent spot on the head (the "one-spot clade"). *Stictolethaeus* is excluded from this group because it retains the presumed plesiomorphic condition of two iridescent head spots. Of the 6 Neotropical genera that possess two iridescent spots, *Stictolethaeus slateri* superficially resembles *Esuris terginus* Stål, which is also coleopteroid and heavily punctate. The iridescent spots of *Esuris terginus* are quite unlike those of *Stictolethaeus slateri.* In the former they are composed of a field of overlapping pegs, whereas in the latter they are composed of ridges. The only other lethaeine taxon with two iridescent head spots composed of ridges is *Bubaces* Distant, with several Neotropical species. In all species of *Bubaces,* each spot as 3 ranks of parallel ridges with profiles that appear rounded at higher magnification (Fig. 5). Each spot in *Stictolethaeus slateri,* however, is a single, crescent-shaped rank of angulate ridges (Fig. 4). Since the shape and fine structure of each spot are so different, I do not consider them homologous.

The deep notch in the dorsal margin of the metathoracic scent gland evaporative area is also found in some species of *Cryphula* Stål and an undescribed genus, both of which are members of the unrelated one-spot clade of Neotropical Lethaeini. For this reason, I assume that the notched condition has arisen more than once.

Stictolethaeus slateri also exhibits several autapomorphies. The male has a sperm resevoir unique in the Lethaeini, and nothing even vaguely like it is known elsewhere in the Rhyparochrominae (O'Donnell, 1979). The female spermatheca has an unusual, asymmetrical sclerite between the bulk and flange. The fusion and modification of the terminal abdominal segments of the female are also unlike anything previously described in the tribe. Still another autapomorphy is the sexually dimorphic adult abdomen. In the female, terga anterior to scent-gland scar 3–4 are almost entirely desclerotized (Fig. 16). In the male, the anterior terga are not as desclerotized, and all terga under the hemelytra are covered with pores that extend right through the cuticle (Figs. 6, 7). These openings suggest dermal gland ducts (Hadley, 1986), although I was unable to confirm this. The female shows no sign of these pores (Figs. 8, 9). If these pores do indeed indicate openings of ducts from dermal glands, their presence only in the male suggests an interesting function for whatever substance, presumably a pheromone, is secreted.

The nymph also shows distinctive autapomorphic characteristics. The convergent anterior dorsal abdominal scent gland canals in the nymph are especially intriguing because tergum 4 is very reduced between them, yet sternum 4 appears of normal size in both the immature and the adult. The fifth instar nymph also has two fully-developed iridescent spots on the head, of the same type as the adult. This is the first information available on the ontogeny of this structure.

All of the adult specimens examined are coleopteroid in the sense of Slater (1975). Features often associated with coleoptery, and found in *Stictolethaeus slateri,* include loss of the hind wing, desclerotization of the anterior abdominal tergites in the female and perhaps the loss of innerlaterotergites. In contrast, ocelli, which are frequently lost in coleopteroid lygaeids, are present in *Stictolethaeus slateri.* Although modified forewings are relatively common in ground-living lygaeids, coleoptery and other extreme wing forms are less common. These types of wings are usually associated with xeric or montane habitats or islands (Slater, 1977, 1985), where the degree and relative frequency of such modifications are correlated with habitat permanence

(Sweet, 1964; Slater, 1977 and references therein). It remains to be seen whether or not the lygaeid fauna of the pampa grasslands will fit these general patterns.

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TWO NEW SPECIES OF *CALIOTHRIPS* (THYSANOPTERA: THRIPIDAE) AND A KEY TO THE NEARCTIC SPECIES

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Abstract.—Two new species of *Caliothrips, C. floridensis* and *C. multistriatus,* are described from the United States. *Caliothrips insularis* (Hood) is a new record for the United States. A key is provided for ten Nearctic species.

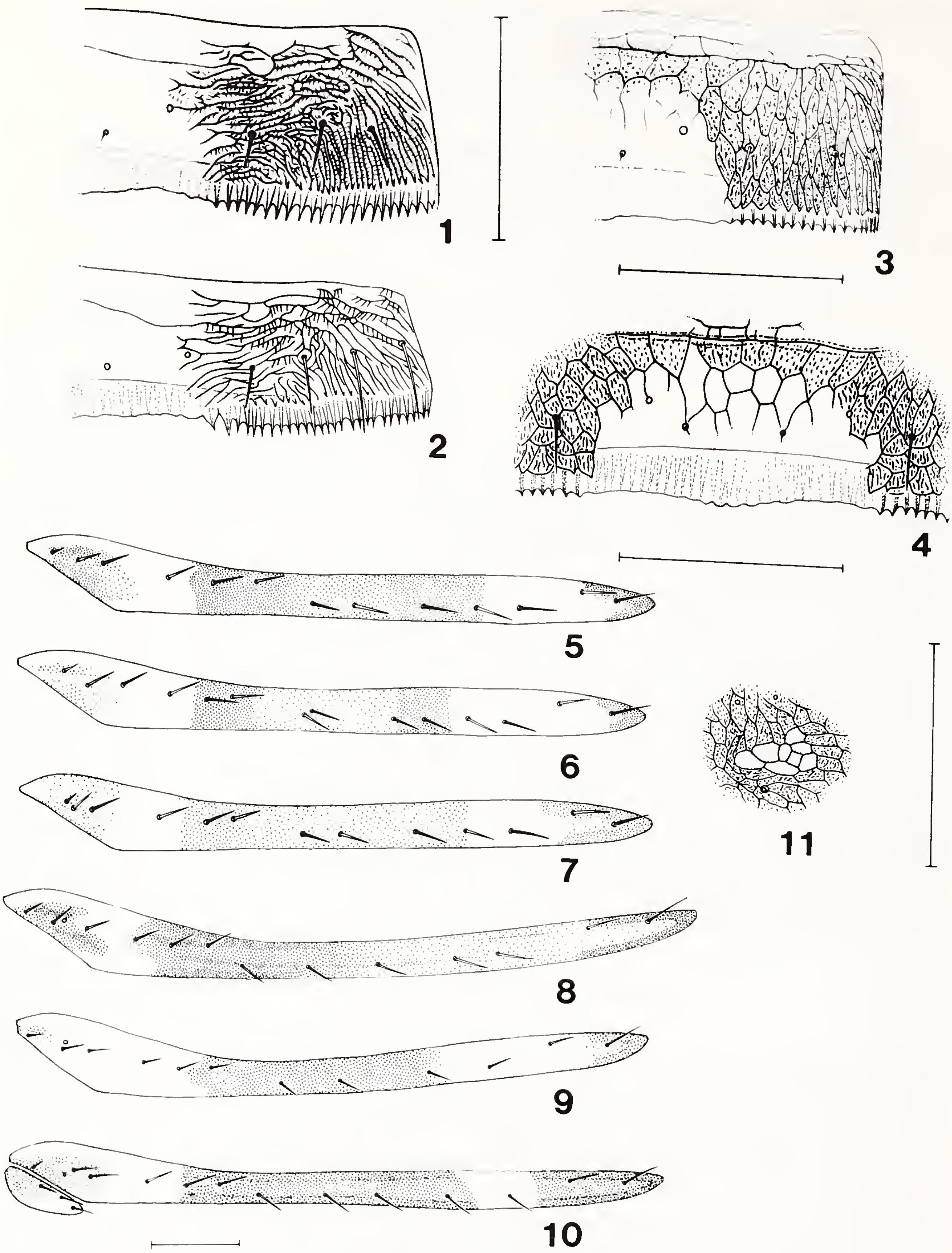
The genus *Caliothrips* was reviewed by Wilson (1975) in his monograph of the subfamily Panchaetothripinae (Thripidae). He treated 18 species of the world including eight species from the Nearctic Region. Of the eight species, *C. fasciatus* (Pergande) and *C. phaseoli* (Hood) are pests of agricultural crops (Ananthakrishnan, 1984; Bailey, 1937). In this paper two new species are described, *C. floridensis* from Florida, and *C. multistriatus,* previously misidentified as *C. phaseoli* from southeastern United States. *Caliothrips insularis* (Hood) is a new record for the United States and its known distribution and host plants are given. A key is provided for the 10 species in the Nearctic Region.

The acronyms for the depositories of examined material are: Natural History Museum, London (NHM); California Department of Food and Agriculture, Sacramento (CDFA); Florida State Collection of Arthropods, Gainesville (FSCA); Forschungsinstitut Senckenberg, Frankfurt am Main, Germany (FS); Georgia Station, University of Georgia, Griffin (GSG); United States National Museum of Natural History (USNM) (collection located at Beltsville, Maryland).

Caliothrips floridensis, new species
Figs. 3, 10, 11

Female: Body dark brown; head completely brown with ocellar crescent reddish orange; legs with tarsi yellow, most of femora and tibiae brown with bases and apices yellow. Forewings with basal brown area, broad median brown band about ½ as long as wing, and shorter apical brown band; subapical pale band about ½ as long as apical brown band (Fig. 10); all setae pale. Antennae brown except III and IV yellow with brown shade medially by subapical setae, most of V yellow, pedicel of VI pale.

Head slightly wider than long, completely reticulated; reticles on median part of head with wrinkles, posterior reticles mostly with short lines and raised dots; 3–4 rows of reticles along posterior margin of head differentiated from rest of reticles, posterior row with small raised dots, anterior with sparse small raised dots or weakly indicated wrinkles; ocellar setae III anterior of posterior ocelli, ocellar setae II anterolaterad of anterior ocellus; postocular setae 2 pairs, transversely aligned, lateral



Figs. 1–11. *Caliothrips* spp. 1–4. Abdominal tergite IV. 1. *C. multistriatus.* 2. *C. phaseoli.* 3. *C. floridensis.* 4. *C. insularis.* 5–10. Forewings. 5. *C. phaseoli* (darker median brown band). 6. *C. phaseoli* (paler median brown band). 7. *C. multistriatus.* 8. *C. insularis.* 9. *C. cinctipennis.* 10. *C. floridensis.* 11. Reticulations on median part of pronotum of *C. floridensis.* (Scale for all figures = 0.1 mm.)

pair near posterior margin of eye. Antennal segment II subglobular, wider than other segments, segments III–IV strongly constricted distally, III slightly longer than IV, VIII subequal to VI. Pronotum transverse, completely reticulated; reticles on pronotum mostly with raised dots and short lines (Fig. 11). Mesonotum without reticulations anteriorly; medially reticulated, reticles with raised dots and short lines; sculpture lines between median setae converging posteriorly, short lines between converging lines. Forewings with 20–21 costal setae, slightly shorter than anterior fringe cilia and longer than width of wings at midlength; forevein with basal setae in two groups of 3 and 3 setae, and 2 distal setae; hindvein with 5 setae. Abdominal tergites (Fig. 3) reticulated except reticulations in median part absent posterior of median setae on intermediate and posterior tergites, median reticles on anterior ½ of tergites with numerous small raised dots; reticles on lateral ⅓ mostly with small raised dots and few short lines; sternites polygonally reticulated; segment IX about twice as long as X, dorsal split about ⅔ as long as tergite X.

Male: Not available.

Measurements of holotype: Body length 1.41 mm. Forewing length 795–812 μm, width at midlength 40–44 μm. Median length of abdominal tergite IX 153 μm, median length of abdominal tergite X 72 μm.

Total length of antenna 252 μm (based on a paratype); segment I 17(24) μm, II 37(35) μm, III 47(22) μm, IV 40(22) μm, V 37(22) μm, VI 32(22) μm, VII 12(8) μm, VIII 30(6) μm. The length of the antennal segment is given first and the width is in parentheses.

Material: Holotype and 4 paratype females; Hilliard, Florida, sweeping, 5-X-38, F. Andre (USNM).

Etymology: Named after Florida, the only state where the species is known to occur.

Comments: This species closely resembles *cinctipennis* but is readily differentiated by the shorter subapical pale band on the forewings.

For the measurement of the antenna, a paratype was used because the basal antennal segments of the holotype are tilted and they could not be measured accurately.

Caliothrips insularis (Hood)
Figs. 4, 8

Hercothrips insularis Hood 1928:234.
Heliothrips bruneri Morgan 1929:8; Hood 1940:37.
Caliothrips insularis: Medina Gaud 1961:58; Wilson 1975:85.

Distribution: United States (Florida). Other countries: Bermuda, Brazil, Cuba, Dominican Republic, Grenada, Martinique, Mauritius, Panama, Puerto Rico, St. Croix, St. Lucia, Tobago, Trinidad, Venezuela.

Hosts: *Cymbopogon* sp. (lemon grass), *Cyperus esculentus,* grasses, *Lilium* sp., *Saccharum officinarum, Setaria barbata, Zea mays.*

Comments: This species has not been recorded previously from the United States. On hand are two specimens collected at Lakeland, Florida on 17 February 1913 on corn leaf and on 18 February 1913 on *Cyperus esculentus* by G. G. Ainslie.

Caliothrips multistriatus, new species
Figs. 1, 7

Caliothrips phaseoli (Hood): Wilson 1975:92.

Female body brown, except head brown in posterior ½, yellowish brown in anterior ½; ocellar crescent orange-red. Legs with tarsi yellow, femora and tibiae brown in medial ⅓–½, yellow apically and basally. Forewings with brown basal area, broad median brown band and brown apical band; subapical pale band about as wide as apical brown band or shorter; 1 dark seta usually in basal brown area, 1 dark brown seta normally at venal fork, 2–3 on hindvein in median brown band, 0–1 in subapical pale band and 1 in apical brown band (Fig. 7). Antennae brown except III–IV yellow, shaded brown in apical ½, V yellow in basal ⅔.

Head transverse, completely reticulated, reticles with wrinkles; 1–3 rows of reticles along posterior margin differentiated from other reticles, with sparse small raised dots or without marks; ocelli on raised area, ocellar setae III just anterior of posterior ocelli, ocellar setae II laterad of anterior ocellus; postocular setae two pairs. Antennal segment II wider than other segments, III–IV strongly constricted basally and distally, III about 2 times longer than wide, longer than VI; distal constriction of IV about as long as its constricted base. Pronotum twice as wide as long, about as long as head; completely reticulated, reticles on pronotum elongate with wrinkles. Mesonotum bare anteriorly, reticulated medially with wrinkles in reticles, sculpture lines converging posteriorly between median setae. Metanotum reticulated, reticles with wrinkles medially, bare laterally. Forewings with 20–21 costal setae, as long as anterior fringe cilia and longer than width of wing at midlength; forevein with 6 basal setae in two groups of 3 each, and 2 distal setae; hindvein with 3–5 setae. Abdominal tergites reticulated medially on tergite I and in anterior ½ and medially on tergite II, without median reticulations on other tergites; transversely and obliquely striated in lateral ⅓ of tergites with sparse microtrichia on several anterior sculpture lines and numerous wrinkles on interstices between transverse lines and between oblique lines on entire submargin (Fig. 1); segment IX about 1.65–1.75 times longer than X, anterior margin with median notch; irregular dorsal split, occasionally indicated as oval pale area on tergite X.

Males: Similar to females in color and most morphological characters; smaller. Abdominal sternites III–VII each with narrow, transversely elongate glandular areas, slightly narrowed in medial area, slightly curved anteriorly, 8–10 times as wide as long.

Measurements of holotype (female): Length from interantennal process 1.26 mm. Forewing length 779 μm, width at midlength 54 μm. Median length of abdominal tergite IX 86 μm, X 52 μm.

Total length of antenna 272 μm; segment I 27(20) μm, II 37(32) μm, III 52(23) μm, IV 47(22) μm, V 40(22) μm, VI 30(20) μm, VII 12(10) μm, VIII 27(5) μm. The length of the antennal segment is given first and the width is in parentheses.

Measurements of allotype (male): Length from interantennal process to posterior margin of abdominal segment X 1.04 mm. Forewing length 623–635 μm, width at midlength 42 μm. Length of median setae on IX: anterior pair 27 μm, posterior pair 32 μm. Glandular areas on sternites III–VII 54–72 μm wide, about 8 μm long.

Total length of antenna 254 μm; segment I 17(24) μm, II 35(30) μm, III 52(24) μm, IV 44(22) μm, V 40(17) μm, VI 27(20) μm, VII 12(8) μm, VIII 27(5) μm.

Material: Holotype female, allotype male: Henry Co., Georgia, *Lespedeza* sp., 30-X-87, R. Beshear (USNM). Paratypes: 13 females and 2 males with same data as holotype; 1 female, Hilliard, Florida, sweeping, 5-X-38, F. Andre; 4 females, Henry Co., Georgia, southern peas, 30-IX-87, R. Beshear; 14 females and 4 males, Henry Co., Georgia, *Cassia* sp., 30-IX-87, R. Beshear; Hamilton Co., Tennessee, 1 female, grass and weeds, 20-IX-39, F. Turner (39-16383). Depositories of paratypes: BMNH, CDFA, FSCA, FS, GSG, USNM.

Other material: Florida: Gainesville, 3 females, kudzu, 8-VI-21, J. R. Watson (USNM); 1 female, 23-IV-57, F. W. Mead (FSCA); 1 female, *Alysicarpus vaginalis,* 19-X-76, R. L. Crocker (FSCA); 1 female, *Cassia obtusifolia,* 4-IX-87, J. Gillmore (FSCA); 1 female, *Glycine max,* 4-IX-84, R. Hemenway (FSCA). Georgia: Tifton, 5 females, lupine, Fall 1955, C. Benton; 2 females, Fall 1956, C. Benton; 1 female, Winter 1956, C. Benton; 4 females, Fall 1957, C. Benton (58 11882); (USNM). Louisiana: Baton Rouge, 1 female, garden peas, 19-XI-15, C. E. Smith (USNM). North Carolina: Rocky Point, 2 females, *Pisum* sp., 24-XI-43, Wethacry (USNM). Tennessee: 1 male, soil under grass and weeds, 27 and 29-XI-39, F. Turner (39-19124) (USNM).

Distribution: United States (Florida, Georgia, Louisiana, North Carolina, Tennessee).

Hosts: *Alysicarpus vaginalis, Cassia* sp., *C. obtusifolia, Glycine max,* grass, *Lespedeza, Lupinus, Pisum, Pueraria thunbergiana,* southern peas.

Etymology: Specific ephithet derived from Latin "multus" and "stria" for the numerous wrinkles between the sculpture lines on the abdominal tergites.

Comments: Wilson (1975) treated specimens with an uniform brown median band on the forewings from Florida and Georgia as a color variation of *phaseoli.* I have examined these specimens as well as other specimens with uniform brown median band on the forewings from Florida, Georgia, Louisiana, North Carolina and Tennessee and conclude that they represent a new species, *multistriatus.* This species is similar to *phaseoli* except the forewings have an uniform brown median band, and numerous wrinkles are present between the sculpture lines on entire lateral ⅓ of abdominal tergites II–VII; conversely, *phaseoli* differs by the median brown band on the forewings either pale brown or almost completely white medially with two submedial brown bands, and by lacking wrinkles on the interstices on the lateral ⅓ of the tergites.

KEY TO NEARCTIC SPECIES OF *CALIOTHRIPS* (FEMALES)

1. Submargins of abdominal tergites transversely and obliquely striated, interstices with microtrichia, wrinkles or glabrous (Figs. 1, 2) 2

– Submargins of abdominal tergites polygonally reticulated, with wrinkles, short lines and/or small raised dots in reticles (Figs. 3, 4) 4

2(1). Forewings lacking basal brown area; 2–3 stout, dark brown setae at region of venal fork; subapical pale band with pale setae; base of antennal segment VI yellow .... *striatus* (Hood)

– Forewings with basal brown area (Figs. 5, 6), usually one dark brown seta at region

of venal fork; subapical pale band normally with 1 brown seta; antennal segment VI brown 3

3(2). Forewing (Figs. 5, 6) with median brown band lighter brown to almost completely pale medially with proximal and distal parts darker brown; subapical pale band usually wider than apical brown band; submarginal sculpture on lateral ⅓ of abdominal tergites with microtrichia only (Fig. 2), cephalad of dorsal setae .... *phaseoli* (Hood)

– Forewing with uniform brown median band (Fig. 7) except proximal part of band usually slightly darker brown; subapical pale band about as wide as apical brown band; numerous wrinkles in interstices between transverse lines and oblique lines on entire lateral ⅓ of abdominal tergites V–VII (Fig. 1) .... *multistriatus,* n. sp.

4(1). Forewings white except for brown apex and occasional pale brown blotch in basal ¼; antennal segments III–V predominantly yellow, shaded pale brown apically on III–V; legs yellow completely or shaded brown medially on femora and tibiae .... *punctipennis* (Hood)

– Forewings with brown crossbands or band along posterior margin; other characters various 5

5(4). Forewings with narrow brown band along posterior margin distally from sub-basal brown crossband, recurved at apex along anterior margin to about subapical venal seta; venal setae pale yellow; antennal segment III yellow in proximal ½, IV–V yellow in proximal ⅓ .... *marginipennis* (Hood)

– Forewings crossbanded; venal setae in brown band normally brown; color of antennae various 6

6(5). Forewings each with three brown crossbands in addition to subbasal brown spot .... *fasciapennis* (Hinds)

– Forewings with not more than two brown crossbands in addition to sub-basal brown spot 7

7(6). Pronotum with wrinkles in reticles; abdominal tergites III–V with medial reticulations absent or present in anterior ⅓; antenna brown, except III–IV yellow with medial ⅓ brown, V yellow at base .... *fasciatus* (Pergande)

– Pronotum with raised dots and short lines in reticles (Fig. 11); abdominal tergites III–V completely reticulated medially or reticulations extending to median setae (Figs. 3, 4); antennal segments III–V yellow with distal ½ partially shaded pale brown 8

8(7). Forewing with median uniform brown band, abruptly separated from apical brown band by pale band; abdominal tergites mostly with small raised dots in reticles (Fig. 3) 9

– Forewing with median band dark brown at proximal part, gradually paler brown distally, pale brown or pale before darker brown apex (Fig. 8); abdominal tergites mostly with short lines and wrinkles in reticles (Fig. 4) .... *insularis* (Hood)

9(8). Forewings with subapical pale band as wide or wider than apical dark band (Fig. 9); anterior part of head yellowish brown; antennal segment I yellow basally, brown distally, base of VI often yellow .... *cinctipennis* (Hood)

– Forewings with subapical pale band shorter than apical dark band (Fig. 10); head completely brown; antennal segment I brown, VI brown .... *floridensis,* n. sp.

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THE TRIBE OPISTHIINI (COLEOPTERA: CARABIDAE): DESCRIPTION OF THE LARVAE, NOTE ON HABITAT, AND BRIEF DISCUSSION ON ITS RELATIONSHIPS

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Abstract.—All instar larvae of *Opisthius richardsoni* Kirby, 1837 and the first and second instar larvae of *Paropisthius indicus* (Chaudoir, 1863) are described and the character states of the tribe Opisthiini are highlighted. The two species differ mainly by the shape of the nasale, length of the antennae, shape of the seta TE_{10} on tergites VII and VIII, and the presence or absence of secondary setae on the tarsi. The adults of *O. richardsoni* are strictly riparian, occurring mainly on sandy or clayish-sandy banks of rivers. Those of *P. indicus* occur at high elevations (3,000–3,900 m) on well-drained substrate in open habitats, away from water. The larvae of both species can jump vigorously when disturbed. The analysis of the character states of the known larvae of Nebriitae does not support the accepted classification of the group based on the character states of the adults.

The Opisthiini form a small tribe of primitive carabids. The adults look superficially like members of the genus *Elaphrus* Fabricius, because of their elytral sculpture, and the tribe has been classified near the Elaphrini by some 19th century authors. Many character states, however, clearly show that the Opisthiini belong to the nebrioid complex. Only five species of Opisthiini have been described to date: *Opisthius richardsoni* Kirby, 1837 which occurs in western North America, from the Prairies to the Pacific Coast (Lindroth, 1961), and four species of *Paropisthius* Casey, namely *P. indicus* (Chaudoir, 1863) from the Himalaya, *P. unctulus* Andrewes, 1932 from North Kumaon in the Indian state of Uttar Pradesh, *P. davidis* (Fairmaire, 1887) from the Chinese province of Yunnan, and *P. masuzoi* Kasahara, 1989 from Taiwan.

Until fairly recently, opisthiine larvae were unknown. Gardner (1954), Lindroth (1960) and Thompson (1979) described those of *O. richardsoni,* based on specimens collected in the field. The purpose of this paper is to describe the larvae of both genera of Opisthiini, add information on the bionomics of these species, and briefly discuss the relationships of the tribe.

MATERIALS AND METHODS

The description of *Opisthius richardsoni* is based on 18 larvae ($12L_1$, $4L_2$, $2L_3$) reared *ex ovo* from adults collected at Edmonton, Alberta, Canada; that of *Paropisthius indicus* is based on 10 larvae ($8L_1$, $2L_2$) reared *ex ovo* from adults collected by the junior author above Syabru (3,700–3,900 m), Rasuwa District, Nepal. Larvae are deposited in the Canadian National Collection, Ottawa.

About half of these specimens have been cleared in hot 10% KOH, impregnated with glycerine (see Goulet, 1977), and studied with an interference contrast microscope at 100–400×. The remaining specimens were studied superficially in ethanol using a stereoscopic microscope at 40–80×.

Terms used for structures have been explained previously (Bousquet, 1985; Bousquet and Smetana, 1986). The notation of primary setae and pores follows that of Bousquet and Goulet (1984).

In addition to larvae of Opisthiini, those of a few species of *Nebria* Latreille, *Leistus* Frölich, and *Notiophilus* Duméril were also studied. Information on larvae of *Pelophila* Dejean was taken from Andersen (1970) and Luff (1972).

TRIBE OPISTHIINI

Diagnosis. The larvae of Opisthiini differ from those of most other carabid groups by the combination of the following character states: head not constricted; antennomere III with numerous setae; urogomphi long, articulated to tergite IX; and leg with 2 unequal claws.

Description. First instar: *Microsculpture.* Parietale dorsolaterally with meshed microsculpture, sculpticells somewhat scalelike. Discal area of pronotum with meshed microsculpture, sculpticells scalelike. Discal area of mesonotum and metanotum mostly with multipointed microsculpture. Discal area of tergites I–IX with pointed and multipointed microsculpture. Urogomphi with strong pointed microsculpture. Pygidium with pointed microsculpture.

Chaetotaxy. Setae FR_1, FR_3, FR_4 and FR_6 on frontale moderately long, about 0.5 length of seta FR_2; seta FR_1 located in front of FR_2. Setae PA_4 and PA_8 on parietale moderately long, clearly longer than PA_1–PA_3; seta PA_5 small, about same size as PA_3; seta PA_8 anteriad to level of seta PA_9; seta PA_6 close to posterior row of stemmata. Antennomere III with numerous additional setae (Fig. 4). Setal group gMX of maxilla with about 30 setae (Fig. 6); seta MX_2 located on anterior half, shorter than MX_3; seta MX_6 on lacinia very small, laterad; maxillary palpomere III with 4 setae (including MX_{11} and MX_{12}). Seta LA_4 on prementum absent. Setae PR_2, PR_3, PR_6, PR_9, PR_{10}, PR_{11}, PR_{12} and PR_{14} on pronotum moderately long, more or less subequal in length; seta PR_8 indistinct. Setae ME_1, ME_8*, ME_9, ME_{11}, ME_{12} and ME_{13} on mesonotum and metanotum moderately long, more or less subequal in length; seta ME_2* indistinct. Setae TE_1, TE_7, TE_9 and TE_{10} on tergites I–VIII moderately long, more or less subequal in length (except TE_{10} on tergites VII and VIII in *Paropisthius*); seta TE_6 indistinct. Seta UR_2 on tergite IX moderately long; seta UR_3 very small, porelike; setae UR_4–UR_8 on urogomphi moderately long; seta UR_4 located near middle of urogomphus. Seta FE_6 spiniform as FE_2–FE_5; setae UN_1 and UN_2 on claws very small.

Head. Cephalic capsule (Fig. 4) subquadrate or transverse. Egg-bursters consisting of longitudinal carina at each side of frontale, extending from base to level of FR_1; nasale (Figs. 2, 3) not prominent, with 4 toothlike processes; adnasale not prominent; frontal suture V-shaped; coronal suture relatively long, its length at least 0.7× that of antennomere I. Parietale with 6 stemmata, in two rows of 3, on each side; cervical and ocular grooves absent. Antenna (Fig. 4) same length or longer than mandible; sensorial appendage on antennomere III rather small, located ventrally at apex. Mandible (Fig. 4) moderately curved; terebra with medial margin smooth; retinaculum well-developed, located just behind middle, its posterior margin smooth; penicillum present, consisting of many setae. Stipes (Fig. 6) elongated, about 2.2× as long as wide, with narrow membranous notch on lateral half of ventral side; lacinia present, strongly acuminated apically; galea 2-segmented, both segments subequal

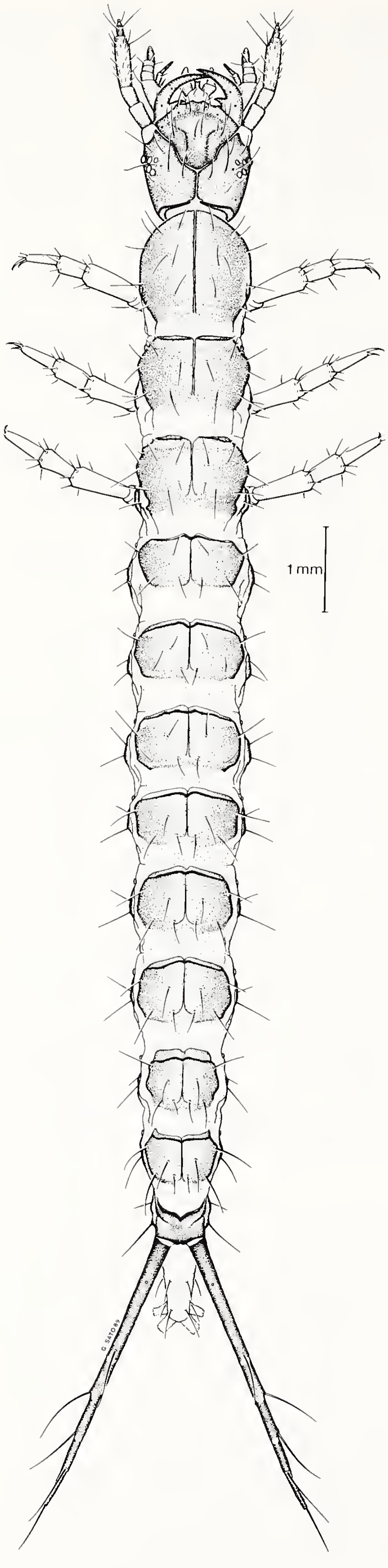


Fig. 1. Larva of *Paropisthius indicus* Chaudoir, L_1.

in length; palpomeres I, II and III short, subequal in length, palpomere IV about 3× longer than other palpomeres. Prementum (Fig. 5) subquadrate; ligula present, wide, as long as palpomere I, with apical margin slightly notched medially; palpomere I shorter than palpomere II.

Thorax. Notal carina indistinct.

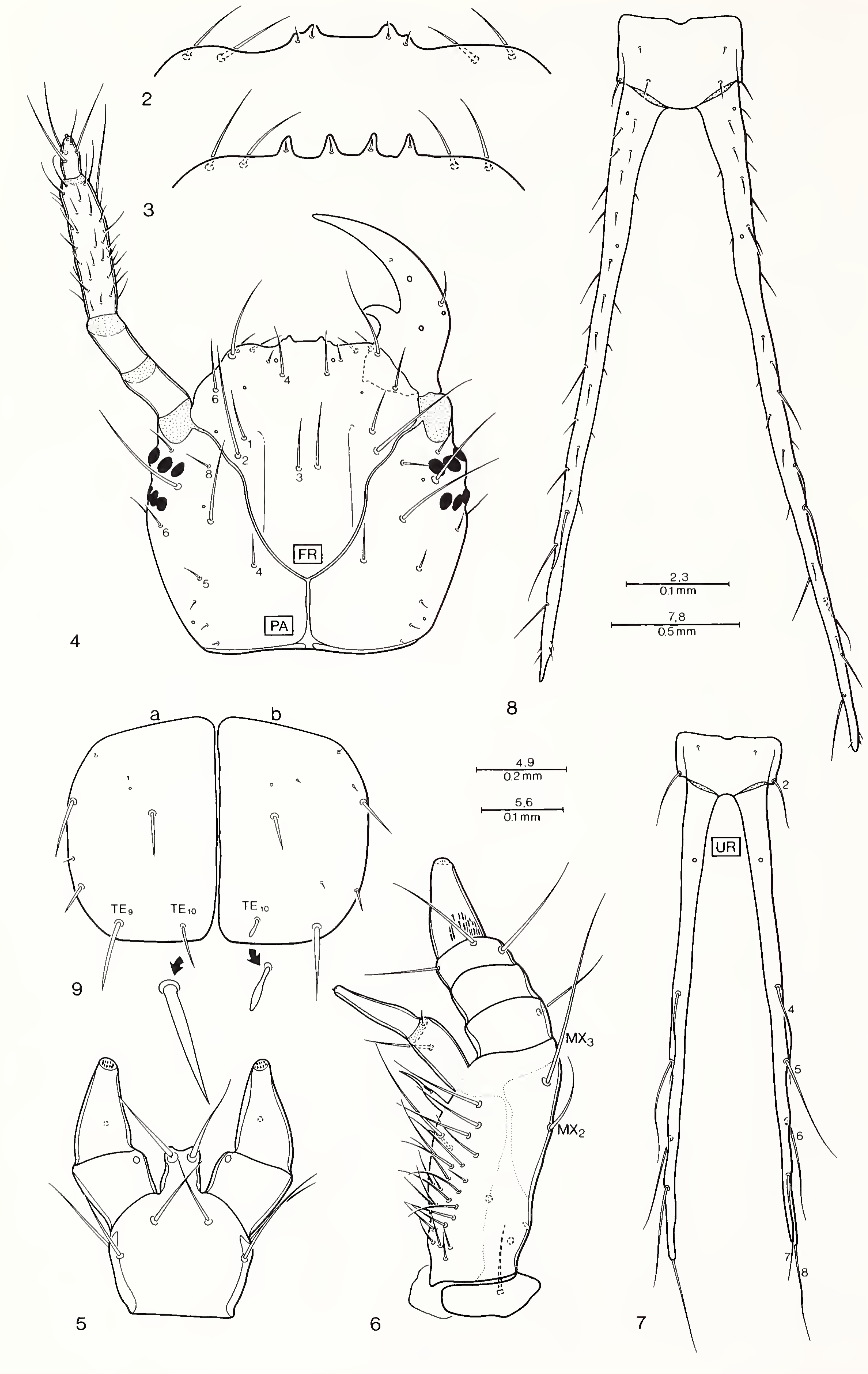
Abdomen. Tergal carina indistinct on all segments. Urogomphi (Fig. 7) long, 7–9× as long as tergite IX, thin, articulated, usually slightly divergent posteriorly, not segmented but with small, narrow unsclerotized bands under levels of setae UR_4, UR_5, UR_6 and UR_7. Pygidium elongated, with tergum and sternum distinct. Pleura of segment I with small invaginated structure (distinct only under compound microscope) near hypopleurite. Epipleurites distinct on segments I–IX; hypopleurite small, poorly pigmented (especially in *Opisthius*) and often more or less distinct.

Legs. Legs rather long; tibia shorter than femur; tarsus subequal to femur; claws unequal, anterior one longer and about 0.6× length of tarsus.

Second instar: *Microsculpture.* Discal area of tergites I–VIII with mainly multipointed microsculpture. Urogomphi with strong, pointed microsculpture all over. Pygidium with multipointed microsculpture all over.

Chaetotaxy. Antennomere I with 1 medial seta, antennomere II with 3 apical setae; antennomere III with numerous setae; antennomere IV without secondary setae. Mandible with 1 small secondary seta posterior to MN_1. Stipes without secondary setae laterally; seta MX_2 located on anterior half; gMX with about 40 setae, most setae of gMX on anterior half bigger than remaining ones; seta MX_6 on lacinia very small; galeomeres and palpomeres I, II and IV without secondary setae; palpomere III with 4–5 setae apically. Prementum with 2–4 secondary setae on each side; seta LA_4, absent; labial palpomeres without setae. Pronotum, mesonotum and metanotum with few (less than 10), small, secondary setae on each side. Tergites I–VIII with 1–4 small secondary setae on each side; setae TE_1, TE_7 and TE_9 moderately long, subequal in length; seta TE_6 very small, about same size as TE_4. Tergite IX with 1–3 secondary setae each side near base of urogomphi; seta UR_2 on tergite IX about same size as secondary setae on urogomphi; seta UR_3 very small. Urogomphus with 20–25 secondary setae, most of them on basal half; most secondary setae smaller than primary setae UR_4–UR_8. Epipleurite with 4–6 small, secondary setae; hypopleurite with 2–4 small, secondary setae. Pygidium with about 20 small, secondary setae on sternite. Femur with about 10 small, secondary setae; tibia with 0–3 small, secondary setae.

Head. Cephalic capsule transverse. Nasale not prominent, with 4 toothlike processes; adnasale not prominent; frontal suture V-shaped; coronal suture distinct, its length 0.6–0.8× that of antennomere I. Parietale with 6 stemmata, in two rows of 3, on each side; cervical and ocular grooves absent. Antenna subequal or longer than mandible; sensorial appendage on antennomere III rather small, located ventrally at apex. Mandible moderately curved; terebra with medial margin smooth; retinaculum well-developed, located just behind middle, its posterior margin smooth; penicillum present, consisting of many setae. Stipes elongated, about 2.2× as long as wide, with narrow membranous notch on lateral half of ventral side; lacinia present, strongly acuminated apically; galea 2-segmented, segments subequal in length; palpomeres I, II and III short, subequal in length, palpomere IV 2.5–3.0× longer than other palpomeres. Prementum subquadrate; ligula present, wide, nearly as long as palpomere


2
3
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0.1 mm
MX3
MX2
UR
5
6
7

I, with apical margin notched medially; palpomere I slightly shorter than palpomere II.

Thorax. Notal carina distinct or indistinct.

Abdomen. Tergal carina indistinct on all segments. Urogomphi (Fig. 8) long, 6–9× as long as tergite IX, thin, articulated, usually divergent posteriorly, not segmented but with 4–5 small, narrow, unsclerotized bands on posterior half. Pygidium elongated; apical folds without conspicuous crochets.

Legs. Legs rather long; tibia shorter than femur; tarsus subequal in length to femur; claws unequal, anterior one longer and about 0.6× length of tarsus.

Third instar[1]: Same as second instar except for the following character states.

Chaetotaxy. Antennomere I with 2 medial setae; antennomere II with 4–5 apical setae. gMX on stipes with more than 40 setae. Pronotum with about 20 distinct secondary setae (at 40× under stereo microscope); mesonotum and metanotum with about 10 distinct secondary setae (at 40× under stereo microscope). Tergite I–VIII with 5–7 distinct secondary setae (at 40× under stereo microscope); seta TE_6 moderately long, longer than TE_4.

Head. Length of coronal suture 0.4–0.5× that of antennomere I. Antenna subequal in length to mandible. Stipes about 2.4× as long as wide. Maxillary palpomere IV about 2.0× longer than palpomere III. Labial palpomeres subequal in length.

Thorax. Notal carina indistinct.

Abdomen. Urogomphi about 5× as long as tergite IX.

Paropisthius indicus Chaudoir, 1863

Diagnosis. The larvae of this species are easily distinguished from those of *Opisthius richardsoni* by having the lateral toothlike processes of the nasale in contact with the medial ones (Fig. 2), the antennae distinctly longer than the mandibles (Fig. 4), and setae TE_{10} on tergites VII and VIII thin and spatulate apically (Fig. 9*b*). In the second instar, the species is also recognized by the presence of secondary setae on the tarsi.

The third instar is unknown, but it will likely differ from the third instar of *O. richardsoni* by the same diagnostic character states as those mentioned for the first and second instars.

Description. First instar: *Chaetotaxy.* Length of seta PR_{13} on pronotum 0.2–0.3× that of PR_{12}. Seta TE_{10} on tergites VII and VIII thin, spatulate apically (as in Fig. 9*b*). *Head.* Cephalic capsule subquadrate (length/width ratio about 1). Nasale with lateral toothlike processes in contact with medial ones (Fig. 2). Length of coronal suture about 1.2× that of antennomere I. Antenna longer than mandible (Fig. 4); length of antennomere I about 1.1× that of antennomere II, about 0.4× that of antennomere III, and about 1.6× that of antennomere IV. Apical margin of ligula

[1] The description is based on the examination of *Opisthius* larvae only.

←

Figs. 2–9. Larva of *P. indicus* (except Figs. 3 and 9*a*). 2. nasale, L_1; 3. nasale of *Opisthius richardsoni*, L_1; 4. Cephalic capsule, left antenna, and right mandible, L_1; 5. prementum (dorsal view), L_1; 6. maxilla (dorsal view), L_1; 7. urogomphi and ninth tergite, L_1; 8. urogomphi and ninth tergite, L_2; 9. Tergite VIII of *O. richardsoni* (*a*) and *P. indicus* (*b*), L_2.

slightly notched medially (Fig. 5). *Abdomen.* Length of urogomphi about 9× that of tergite IX (Fig. 7).

Second instar: *Microsculpture.* Microsculpture on frontale poorly impressed. *Chaetotaxy.* Frontale without distinct secondary setae (at 40× under stereo microscope). Seta TE_{10} on tergites VII and VIII thin, spatulate apically, distinctly smaller than TE_9 (Fig. 9*b*). Tarsus with about 10 secondary setae. *Head.* Cephalic capsule slightly transverse, (length/width ratio about 0.9). Nasale with lateral toothlike processes in contact with medial ones (as in Fig. 2). Length of coronal suture about 0.8× that of antennomere I. Antenna distinctly longer than mandible; antennomere I subequal to antennomere II, about 0.5× length of antennomere III; antennomere III about 5.5× length of antennomere IV. Apical margin of ligula slightly notched medially (as in Fig. 5). *Thorax.* Notal carina distinct. *Abdomen.* Urogomphi longer, length about 8–9× that of tergite IX (Fig. 8). *Legs.* Legs proportionally longer.

Third instar: Unknown.

Measurements. Head width: 0.69–0.75 mm (L_1; n = 8); 0.91 mm (L_2; n = 2).

Opisthius richardsoni Kirby, 1837

Diagnosis. The larvae of this species differ from those of *Paropisthius indicus* mainly by the separated and equidistant toothlike processes of the nasale (Fig. 3), the antennae subequal in length to the mandibles, and the unmodified (i.e., not spatulate at apex) setae TE_{10} on tergites VII and VIII (Fig. 9*a*). In the second instar, the species is also distinguished by the absence of secondary setae on the tarsi.

Description. First instar: *Chaetotaxy.* Length of seta PR_{13} on pronotum about 0.6× that of PR_{12}. Seta TE_{10} on tergites VII and VIII unmodified, spiniform (as in Fig. 9*a*). *Head.* Cephalic capsule transverse (length/width ratio about 0.85). Nasale with toothlike processes separated, equidistant (Fig. 3). Length of coronal suture about 0.8× that of antennomere I. Antenna subequal in length to mandible; length of antennomere I about 1.4× that of antennomere II, about 0.6× that of antennomere III, and about 1.3× that of antennomere IV. Apical margin of ligula deeply notched medially. *Abdomen.* Length of urogomphi about 7× that of tergite IX.

Second instar: *Microsculpture.* Microsculpture on frontale distinctly impressed. *Chaetotaxy.* Frontale with distinct secondary setae (at 40× under stereo microscope). Seta TE_{10} on tergites VII and VIII thick, spiniform, slightly shorter than TE_9 (Fig. 9*a*). Tarsus without secondary setae. *Head.* Cephalic capsule distinctly transverse, (length/width ratio about 0.8). Nasale with toothlike processes separated, equidistant (as in Fig. 3). Length of coronal suture about 0.6× that of antennomere I. Antenna subequal in length to mandible; antennomere I about 1.4× length of antennomere II, about 0.7× that of antennomere III; antennomere III about 2.5× length of antennomere IV. Apical margin of ligula deeply notched medially. *Thorax.* Notal carina indistinct. *Abdomen.* Urogomphi smaller, length about 6–7× that of tergite IX. *Legs.* Legs proportionally shorter.

Third instar: Same character states as second instar except for the following. *Head.* Length of coronal suture 0.4–0.5× that of antennomere I. Antennomere III about 4× length of antennomere IV. *Abdomen.* Urogomphi about 5× length of tergite IX.

Measurements. Head width: 0.63–0.67 mm (L_1; n = 10); 0.80–0.84 mm (L_2; n = 4); 1.06–1.09 mm (L_3; n = 2).

BIONOMICS

Adults of *Opisthius richardsoni* are strictly riparian. They occur on sandy and gravel banks of large creeks and rivers. According to Lindroth (1960), they prefer habitats close to water "where the soil consists of sand with more or less pronounced mixture of clay and is devoid of higher vegetation." This information concurs with our own observations. However, the association of *Opisthius* with species of the staphylinid genus *Bledius* Mannerheim does not seem to be as constant as postulated by Lindroth (1960). The larvae live in the same habitat as the adults, buried in the soil at least during the daytime; when disturbed, "they perform a most vivid jumping, reminding of that produced by *Piophila* maggots" (Lindroth 1960).

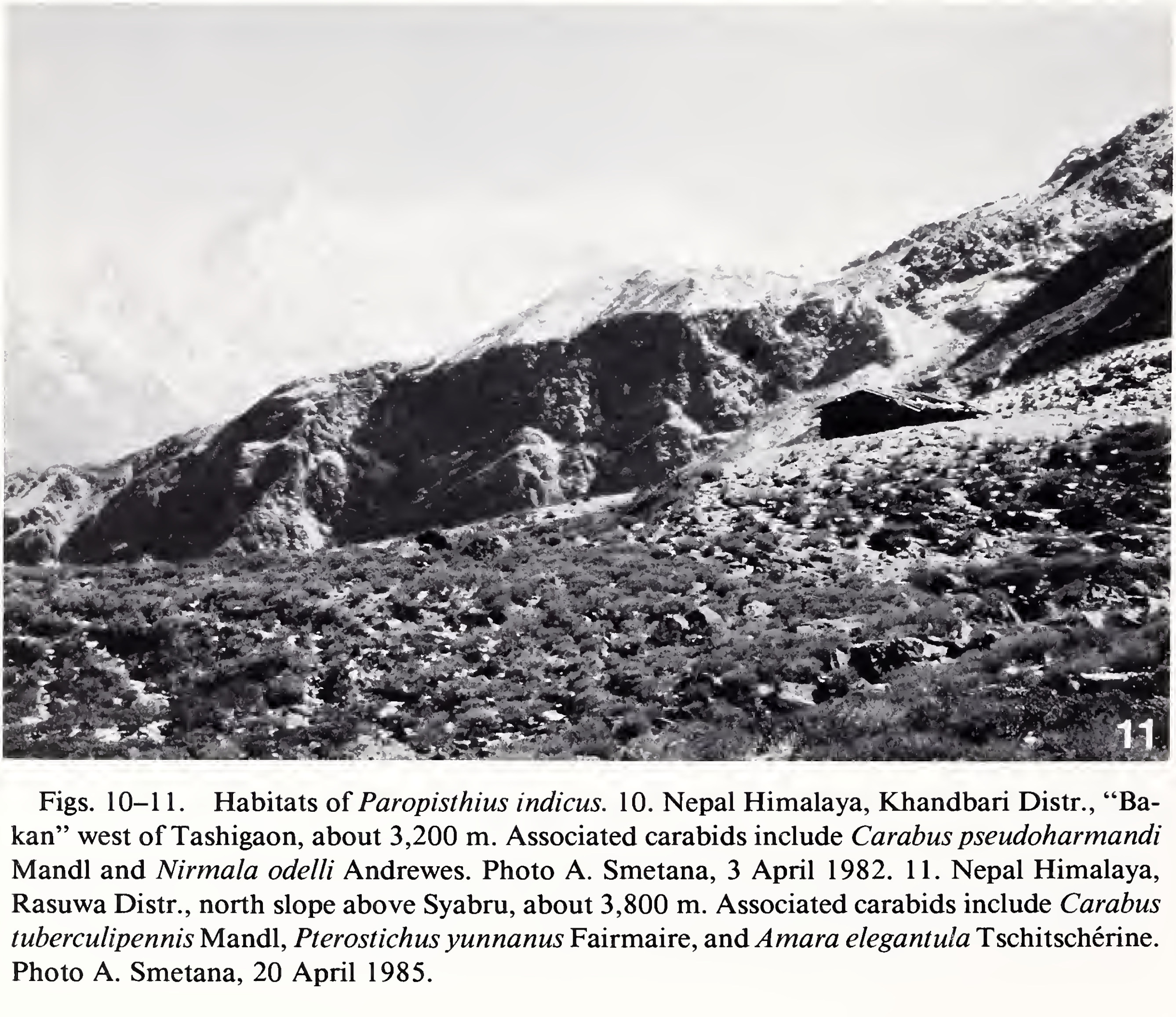
Adults of *Paropisthius indicus* occur away from water. In the Nepal Himalaya, they were collected at high elevations, about 3,000–3,900 m, from the upper zone of the forest to the subalpine zone. They prefer well-drained substrate consisting of sandy soil intermixed with rock debris and sometimes also clay, with little vegetation. Most specimens were collected in open habitats, such as meadowlike pastures, sometimes disturbed by grazing, surrounded by forest (Fig. 10) or on disturbed, dry ground along hiking trails, or in the subalpine zone (Fig. 11) under similar conditions. Adults were frequently observed running on the ground during daytime, especially when the sun was shining. The larvae of *P. indicus* were not found in the field. However, when reared in the laboratory, they displayed behavior similar to that of *O. richardsoni* larvae, jumping vividly up to 10 cm when disturbed. It is assumed that the jumping ability of the larvae of Opisthiini was developed as a defensive mechanism against predators.

According to Kasahara (1989), adults of *Paropisthius masuzoi* are hygrophilous, occurring in very wet places, such as under stones half-immersed in water under small cascades. Nothing is known about the bionomics of *Paropisthius unctulus* and *P. davidis.*

DISCUSSION

The tribe Opisthiini belongs to the supertribe Nebriitae which includes, besides the opisthiines, the tribes Nebriini, Notiokasiini and Notiophilini (Kavanaugh and Nègre, 1982). Erwin (1984, 1985) considered the Cicindisini as belonging to the Nebriitae. However, very little is known about the Cicindisini, which include two rarely collected species—one from the Persian Gulf and the other one from Argentina—and their phylogenetic relationships are still not clearly understood. There seems to be no solid evidence that the Cicindisini are related to the Nebriitae, and for that reason they are not considered further in this discussion.

The Nebriitae (sensu Kavanaugh and Nègre, 1982) is a group represented mainly in the Northern Hemisphere. Notiokasiini—with its single species *Notiokasis chaudoiri* Kavanaugh and Nègre, 1982—is the only lineage represented in the Southern Hemisphere, namely in southeastern South America. Is the supertribe a monophyletic group? Adults Nebriitae share several character states, but, as pointed out by Kavanaugh and Nègre (1982), only one of them—the loss of setae on the parameres—appears apotypic for Carabidae. The character state is of low phyletic weight since it occurs in other unrelated carabid lineages. Two character states shared by larvae of Nebriitae are worth mentioning: the nasale consists of 4 toothlike processes (the



Figs. 10–11. Habitats of *Paropisthius indicus.* 10. Nepal Himalaya, Khandbari Distr., "Bakan" west of Tashigaon, about 3,200 m. Associated carabids include *Carabus pseudoharmandi* Mandl and *Nirmala odelli* Andrewes. Photo A. Smetana, 3 April 1982. 11. Nepal Himalaya, Rasuwa Distr., north slope above Syabru, about 3,800 m. Associated carabids include *Carabus tuberculipennis* Mandl, *Pterostichus yunnanus* Fairmaire, and *Amara elegantula* Tschitschérine. Photo A. Smetana, 20 April 1985.

size and relative position of which vary extensively), and the urogomphi are articulated at the base of the ninth tergite except in the first instar of *Pelophila.* These two character states, although probably apotypic for carabids, still do not strongly support the hypothesis that the Nebriitae is a monophyletic lineage since they occur in other unrelated carabid groups.

Kavanaugh and Nègre (1982) have hypothesized that Opisthiini, based on the presence of two pairs of supraorbital setae in the adults, represent the sister group of the remaining Nebriitae. Larval characters do not support nor do they contradict such an hypothesis. No synapomorphies in the morphology of the larvae have yet been discovered to support the hypothesis that the Nebriini and Notiophilini (the larvae of Notiokasiini are still unknown) form a monophyletic group. However, larvae of Notiophilini and Nebriini, without *Pelophila,* share several apotypic features, such as presence of a well-defined neck, distinctly elongated mandible and retinaculum, and absence of penicillus. Furthermore, larvae of *Leistus* (tribe Nebriini) and Notiophilini have lost the lacinia, another apotypic state within the Carabidae. Immatures of Opisthiini and *Pelophila* (tribe Nebriini) are structurally similar but, as far as we know, do not share any apotypic character states.

Larvae of Nebriitae are little known. Those of Notiokasiini are still unknown and although immatures of most genera (sens. lat.) of Nebriini and Notiophilini have been described, few species in each genus are known. Therefore, any phylogenetic hypothesis concerning the relationships of the groups within the Nebriitae based on larval characters should be evaluated with such limitations in mind. Nevertheless, it is quite clear at this time that the larval characters generally do not support the current classification of the Nebriitae based on adult characters. In fact, the immatures suggest that the Opisthiini and *Pelophila* are both primitive groups that do not share apotypic features, and that the Notiophilini and remaining Nebriini form a monophyletic lineage.

We concur with Kavanaugh and Nègre (1982) that "a significant realignment of tribes and genera will undoubtedly be required when phylogenetic relationships within the supertribe are better understood."

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SYNONYMICAL NOTES ON NORTH AMERICAN PLATYNINI (COLEOPTERA: CARABIDAE), WITH SPECIAL REFERENCE TO NAMES PROPOSED BY T. L. CASEY, AND A REDESCRIPTION OF *AGONUM IMITANS* NOTMAN

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Abstract.—Fifteen species names proposed by T. L. Casey, previously considered valid names of North American *Agonum,* are newly synonymized. The synonymical status of 11 additional species names heretofore considered valid species names of *Agonum* are also reviewed. Twenty-seven new lectotypes are designated. *Olisares* Motschulsky, 1864, is newly syonymized with *Agonum* Bonelli, 1810. *Agonum imitans* Notman, a putative member of the North American fauna, is diagnosed and redescribed.

T. L. Casey (1920, 1924) proposed many species of Platynini now considered invalid. In his treatment of the Canadian and Alaskan carabid fauna, Lindroth (1966, 1975) established the current synonymical status of most such names. Over the past several years I have studied several groups of North American Platynini, and have evaluated many Casey names not included in Lindroth's monograph (Liebherr, 1984, 1985, 1986, 1991). In this paper, I present synonymical notes on the 32 names proposed by Casey that were treated as valid members of *Agonum* in the checklist of Erwin et al. (1977). Lectotypes are designated for 19 of these, and 15 are newly recognized as junior synonyms. Study of type specimens of Chaudoir (1837), Motschulsky (1850, 1864), Bates (1884), Horn (1892), and Notman (1919) has revealed additional unrecognized junior synonyms listed as valid species under the genus *Agonum* in Erwin et al. (1977). The second portion of these notes reports additions and corrections to North American *Agonum* synonymy relative to these names.

Examination of the holotype of *Platynus imitans* Notman (1919) indicates that this species is distinct from all other North American species, and should be placed in the genus and subgenus *Agonum,* sensu Liebherr (1986:177). Notman (1919:233) specified the type locality only as North America, and the geographic origin of the single known specimen has remained in doubt. The species is distinct from all *Agonum* species in Europe (Freude et al., 1976; Jeannel, 1942; Lindroth, 1974, 1986), Japan (Habu, 1978), and South America (unpubl. data). The holotype is redescribed to facilitate recognition of the species, and eventual determination of its geographic provenance.

Based on the new synonymical data presented here, all known species of *Agonum,* sensu Liebherr (1986:177), from North America north of Mexico can now be reliably identified. Lindroth's (1966) key, as modified by Lindroth (1969:1119), Liebherr (1984), and the addition of *Agonum imitans* below, can be used for all species except for those of the *A. extensicolle* group. Liebherr (1986) treats the 7 species of the *A. extensicolle* group.

SYNONYMY OF CASEY NAMES

All Casey specimens listed below are part of the T. L. Casey Collection, deposited in the National Museum of Natural History, Washington, D.C. Species are listed in alphabetical order as presented in Erwin et al. (1977). For each name, a prior lectotype designation is cited, or a new lectotype designation is made. Type localities are given for newly recognized synonyms and for lectotypes. Where original type locality designations are vague, they are restricted to sites from which I have examined specimens. Casey sometimes labeled his specimens with abbreviated state names, e.g., "Cal.", augmented with symbols such as "+", "x", or ".". These symbols, and their positions relative to the letters on the label were keyed to the exact locality within the state; that locality listed as the type locality in his Memoir publications. Therefore, I have listed verbatim label data along with the type locality published by Casey (1920, 1924). All Casey specimens have a "Casey bequest 1925" label above the "Type USNM" label. I have not listed this label in the data below.

Anchomenus amplicollis Casey, 1924:82 = *Agonum fallianum* Leng, 1918 (NEW SYNONYMY); lectotype male hereby designated; type locality Berkeley, CA. Label data: Berkeley, Cal; Jan 17, 1919; Type USNM 47436; Lectotype, Anchomenus amplicollis Casey, J. K. Liebherr 1990.

Agonum angustior Casey, 1920:101 = *Tanystoma maculicolle* Dejean, 1828 (see Liebherr, 1985); lectotype male hereby designated; type locality Hoopa Valley, Humboldt Co., CA. Label data: Cal (a with dot above); ♂; Type USNM 47472; Lectotype, Agonum angustior Casey, J. K. Liebherr 1990.

Anchomenus collisus Casey, 1920:59 = *Agonum elongatulum* Dejean, 1828 (see Liebherr, 1986); lectotype male hereby designated; type locality Marion Co., FL. Label data: Marion County; Fla; Type USNM 47434; Lectotype, Anchomenus collisus Casey, J. K. Liebherr 1990.

Anchomenus concurrens Casey, 1920:49 = *Anchomenus funebris* LeConte, 1854 (see Hatch, 1953); lectotype female hereby designated; type locality Santa Rosa, CA hereby designated. Label data: Cal.; Type USNM 47421; concurrens Casey; Lectotype, Anchomenus concurrens Casey, J. K. Liebherr 1990.

Note: *Anchomenus* Bonelli is a valid genus with type species *Anchomenus dorsalis* Pontoppidan. It comprises 10 species of collective Holarctic distribution, with 4 found in the Pacific states, western Canada, and Baja California (Liebherr, 1991).

Anchomenus cornicula Casey, 1920:51 = *Anchomenus quadratus* LeConte, 1854 (NEW SYNONYMY); lectotype male hereby designated; type locality Hoopa Valley, Humboldt Co., CA. Label data: Cal (a with dot above); ♂; Type USNM 47423; Lectotype, Anchomenus cornicula Casey, J. K. Liebherr 1990.

Anchomenus dissensus Casey, 1920:67 = *Agonum piceolum* LeConte, 1879; lectotype female designated by Lindroth (1975).

Agonum fidele Casey, 1920:116, a valid species (see Lindroth, 1966); lectotype male designated by Lindroth (1975).

Europhilus galvestonicus Casey, 1920:126, a valid species (see Lindroth, 1966); holotype male.

Anchomenus gravidulus Casey, 1920:59 = *Agonum elongatulum* Dejean, 1828 (see

Liebherr, 1986); lectotype female hereby designated; type locality Indian River Haulover, FL. Label data: Haulover, 14 March, Fla: Type USNM 47435; gravidulus Csy; Lectotype, Anchomenus gravidulus Casey, J. K. Liebherr 1990.

Anchomenus impictus Casey, 1920:60 = *Agonum decorum* Say, 1823 (see Liebherr, 1986); lectotype male hereby designated; type locality San Joaquin Co., CA. Label data: San Joaquin Co., CAL; Type USNM 47438; impictus Csy.; Lectotype, Anchomenus impictus Casey, J. K. Liebherr 1990.

Anchomenus luxatus Casey, 1920:67 = *Agonum decorum* Say, 1823 (see Liebherr, 1986); lectotype male designated by Lindroth (1975).

Agonum maculicolle guadalupense Casey, 1920:100 = *Tanystoma maculicolle* Dejean, 1828 (see Liebherr, 1985); lectotype male hereby designated; type locality Guadalupe Island, Baja CA Norte. Label data: Guad. Id.; Type USNM 47471, guadalupense Csy.; Lectotype, Agonum maculicolle guadalupense Casey, J. K. Liebherr 1990.

Micragonum maritimum Casey, 1920:85 = *Agonum crenulatum* LeConte, 1854 (NEW SYNONYMY); lectotype female hereby designated; type locality Galveston, TX. Label data: Tex (x with dot below); ♀; Type USNM 47496; Lectotype Micragonum maritimum Casey, J. K. Liebherr 1990.

Anchomenus morbillosus Casey, 1920:48 = *Anchomenus funebris* LeConte, 1854 (NEW SYNONYMY); lectotype female hereby designated; type locality Redwood Creek, Humboldt Co., CA. Label data: Cal. (a with + above); Type USNM 47419; morbillosus Csy.; Lectotype, Anchomenus morbillosus Casey, J. K. Liebherr 1990.

Anchomenus nevadensis Casey, 1920:48 = *Anchomenus funebris* LeConte, 1854 (NEW SYNONYMY); lectotype female hereby designated; type locality Reno, NV. Label data: Nev (N with dot preceding); ♀; Type USNM 47420; Lectotype, Anchomenus nevadensis Casey, J. K. Liebherr 1990.

Anchomenus opacellus Casey, 1920:50 = *Anchomenus funebris* LeConte, 1854 (NEW SYNONYMY); lectotype female hereby designated; type locality Santa Rosa, CA. Label data: Cal (a with dot beneath); Type USNM 47422; Lectotype Anchomenus opacellus Casey, J. K. Liebherr 1990.

Agonum pacificum Casey, 1920:102, a valid species; lectotype male designated by Liebherr (1984).

Anchomenus parvus Casey, 1920:51 = *Anchomenus funebris* LeConte, 1854 (NEW SYNONYMY); holotype female; type locality Reno, NV.

Micragonum pinorum Casey, 1920:86 = *Agonum crenulatum* Leconte, 1854; lectotype male designated by Lindroth (1975).

Anchus puncticeps Casey, 1920:2 = *Oxypselaphus pusillus* LeConte, 1854, a valid species; lectotype female designated by Lindroth (1975).

Note: *Oxypselaphus* Chaudoir, 1843, is a senior synonym of *Anchus* LeConte, 1854, with type species *O. obscurus* Herbst, 1784 (=*O. pallidulus* Chaudoir, 1843). Lindroth (1966) replaced the specific name *pusillus* LeConte with *puncticeps* Casey due to secondary homonymy in his taxonomically broad concept of *Agonum.* As I consider *Oxypselaphus* generically distinct from *Agonum,* the senior specific name is valid.

Anchomenus renoanus Casey, 1920:51 = *Anchomenus funebris* LeConte, 1854 (NEW SYNONYMY); lectotype male hereby designated; type locality Reno, NV. Label

data: Nev (N with dot preceding); Type USNM 47425; Lectotype, Anchomenus renoanus Casey, J. K. Liebherr 1990.

Circinalia rigidula Casey, 1920:75 = *Agonum rigidulum* Casey, a valid species (see Lindroth, 1966); lectotype male designated by Lindroth (1975).

Anchomenus rugulifer Casey, 1920:33 = *Platynus ovipennis* Mannerheim, 1843 (NEW SYNONYMY); holotype female; type locality Redwood Creek, Humboldt Co., CA.

Note: The single female is teneral. Casey diagnosed this species by color, coarse wrinkles on the dorsum, and flat elytral intervals; all traits often observed in teneral carabids.

Agonum sierranum sequoiarum Casey, 1920:105 = *Agonum subsericeum* LeConte, 1863 (NEW SYNONYMY); holotype female; type locality Redwood Creek, Humboldt Co., CA.

Agonum sierranum Casey, 1920:105 = *Agonum subsericeum* LeConte, 1863 (NEW SYNONYMY); lectotype female hereby designated; type locality Truckee, CA. Label data: Cal. (l crossed with slash); Type USNM 47458; sierranum Csy.; Lectotype, Agonum sierranum Casey, J. K. Liebherr 1990.

Anchomenus solutus Casey, 1920:60 = *Agonum decorum* Say, 1823 (see Liebherr, 1986); holotype female.

Agonum sybariticum Casey, 1920:107 = *Agonum subsericeum* LeConte, 1863 (NEW SYNONYMY); lectotype female hereby designated; type locality southern California, hereby restricted to Lake Henshaw, San Diego Co., CA. Label data: Cal (underlined); Type USNM 47462; Lectotype, Agonum sybariticum Casey; J. K. Liebherr 1990.

Agonum tahoense Casey, 1920:106 = *Agonum cupripenne* Say, 1823 (NEW SYNONYMY); lectotype female hereby designated; type locality Truckee, CA. Label data: Cal. (l crossed with slash); Type USNM 47460; tahoense Csy.; Lectotype, Agonum tahoense Casey, J. K. Liebherr 1990.

Anchomenus tersus Casey, 1920:35 = *Platynus ovipennis* Mannerheim, 1843 (NEW SYNONYMY); lectotype male hereby designated; type locality Redwood Creek, Humboldt Co., CA. Label data: Cal. (a with "x" above); Type USNM 47409; tersus Csy.; Lectotype, Anchomenus tersus Casey, J. K. Liebherr 1990.

Agonum uintanum Casey, 1924:83 = *Agonum cupreum* Dejean, 1831 (NEW SYNONYMY); lectotype male designated by Lindroth (1975); type locality Mammoth, Parowan Mts., UT.

Note: Lindroth (1975:128) stated *A. uintanum* was "probably a subspecies of *cupreum* Dej."

Anchomenus uteanus Casey, 1924:81 = *Agonum decorum* Say, 1823 (see Liebherr, 1986); lectotype male hereby designated; type locality Callao, UT. Label data: Callao, Juab Co., Ut, VI-29-22, Tom Spaldi; Type USNM 47433; uteanus Csy.; Lectotype, Anchomenus uteanus Casey, J. K. Liebherr 1990.

Anchomenus vinnulus Casey, 1920:61 = *Agonum decorum* Say, 1823 (see Liebherr, 1986); lectotype male hereby designated; type locality Battle Mountains, NV. Label

data: Battle Mtn., Nevada; Type USNM 47440; vinnulum Csy.; Lectotype, Anchomenus vinnulus Casey, J. K. Liebherr 1990.

SYNONYMY OF NON-CASEY NAMES

Institutional codes indicate type deposition. The acknowledgments provide complete institutional names. Vague or broadly given type localities are restricted to sites from which I have examined specimens.

Agonum alcyoneum Chaudoir, 1837:24 = *Agonum placidum* Say, 1823 (NEW SYNONYMY). Lectotype male hereby designated (MNHP); type locality Mexico, hereby restricted to Amecameca, Mexico state. Label data: 168; Lectotype (purple border); Lectotype, Agonum alcyoneum Chaud., George E. Ball 1972.

Anchomenus xanthocnemis Bates, 1884:281 = *Agonum propinquum* Gemminger and Harold, 1868 (NEW SYNONYMY). Holotype female (BMNH); type locality Mexico state, Mexico. Label data: Type, H.T. (red circle); Mexico, Salle Coll.; B.C.A. Col. I., 1; Anchomenus xanthocnemis Bates.

Note: *A. propinquum* is reported to have a distribution that is "Transamerican, S at least to New Jersey and Oreg" (Lindroth, 1966:612). I have collected this species in wet pastures in Plumas Co., CA. Although the species as now circumscribed possesses a range containing a 3,100 km disjunction, I have no doubts concerning the identity of the Mexican specimen. As the wet pasture habitat in montane California appears similar to wet habitats in Mexico state, we should expect further collections of this species to be made in wet pasture areas in the intervening regions.

Agonothorax planipennis Motschulsky, 1850:68 (NOMEN DUBIUM). Type apparently lost; type locality Sitka, AK.

Note: This name is not included in Keleinikova's (1976) list of Motschulsky types held at the Moscow State University Collection, suggesting that the type is lost. Motschulsky's (1850:68) terse description may be translated "Like *A. famelicus,* but is somewhat smaller and flatter. The elytra are more weakly striate and with a more metallic reflection." *A. famelicus* Ménétries is a junior synonym of *A. fossigerum* Dejean (see Lindroth, 1966). As the elytral striae, intervals, and metallic reflection vary in *A. fossigerum,* with males often smaller and shinier, Motschulsky's description would be most appropriately attributed to this species. Nonetheless, it is not uncommon for Motschulsky to have mixed widely divergent species-level taxa in his genera, and so I refrain from proposing a formal synonymy. Horn (1892) noted the similarity of Motschulsky's *planipennis* to *Agonum fossigerum,* though he also refrained from formally proposing synonymy of the two names. *A. fossigerum* is distributed from California and western Nevada north to Washington state and southern Alberta, suggesting that Motschulsky's type locality may be in error.

Limodromus acuticollis Motschulsky, 1864:319 = *Platynus tenuicollis* LeConte, 1848 (NEW SYNONYMY). Lectotype male (MSUM) hereby designated; type locality southern states of North America, hereby restricted to Washington, D.C. Label

data: [small pale green square]; sp. Ubia; Limodromus acuticollis Motsch., Amer. bor. [green label]; Lectotype, *Limodromus acuticollis* Motschulsky, J. K. Liebherr 1990.

Note: Keleinikova (1976) lists this single syntype in the Motschulsky collection.

Europhilus iridipennis Motschulsky, 1864:321 = *Badister flavipes* LeConte, 1853: 388 (NEW SYNONYMY). Lectotype female (MSUM) hereby designated; type locality New Orleans, LA. Label data: [small red square]; [larger green circle]; Agonothorax iridipennis Motsch., Am. bor. N. Orl [green label]; Lectotype, Europhilus iridipennis Motschulsky, J. K. Liebherr, 1990.

Note: This name is not included in Keleinikova's (1976) list of Motschulsky types, however N. Nikitsky has sent me a specimen matching the description.

Platynus pterostichoides Bates, 1882 = *Tanystola tropica* Motschulsky, 1864:324 (NEW SYNONYMY). Lectotype male (MSUM) hereby designated; type locality Nicaragua. Label data: Nicaraga (green label); Tanystola tropica Motsch., Nicaragua; red label; Lectotype, Tanystola tropica Motschulsky, J. K. Liebherr 1990.

Note: Keleinikova (1976) mentions this single syntype. Motschulsky's specimen keys to *P. pterostichoides* in Whitehead (1973), and thus the valid combination for this species is *Platynus tropicus* Motschulsky. I join these two names in synonymy at this time to ensure the proper comparison of their respective types when the species group they belong to is revised.

Olisares flavolimbatus Motschulsky, 1864:327 = *Agonum pallipes* F., 1787 (NEW SYNONYMY). Lectotype male (MSUM) hereby designated; type locality Mobile, AL. Label data: red square; green circle; Olisares flavolimbatus Motsch. (green square); red square; Lectotype, Olisares flavolimbatus Motsch., J. K. Liebherr 1989.

Note: In addition to the lectotype there is one female paralectotype labeled "Am. bor." The lectotype has dermestid damage to elytra and abdomen.

I hereby designate *O. flavolimbatus* Motschulsky as the type species of *Olisares* Motschulsky, 1864, making *Olisares* a junior subjective synonym of *Agonum* Bonelli, 1810 (NEW SYNONYMY).

Olisares picipes Motschulsky, 1864:326 = *Agonum punctiforme* Say, 1823 (NEW SYNONYMY). Lectotype male (MSUM) hereby designated; type locality Caracas, Venezuela. Label data: Caraccas (green label); Olisares picipes Motsch., Am. centr. (green label); red label; Lectotype, Olisares picipes Motsch., J. K. Liebherr 1990.

Note: The genitalia and abdominal terga of the lectotype are damaged, and the head is missing, but the specimen agrees with *A. punctiforme* in pronotal configuration, elytral striation, and sternite microsculpture. *A. punctiforme* is distributed from southern Ontario and Quebec south to Texas, California, and Mexico, suggesting that the Caracas locality record may have been the result of accidental introduction or mislabeling.

Platynus arizonensis Horn, 1892:42 = *Agonum cycliferum* Bates, 1884 (NEW SYNONYMY). Lectotype male (MCZ) hereby designated; type locality Camp Grant,

AZ. Label data: Ar; Lectotype 2889 (red label); P. arizonensis Horn; Lectotype, Platynus arizonensis Horn, J. K. Liebherr 1990.

Note: Lindroth (1966:562, 614) includes this species in his treatment of *Agonum*, using the junior name.

Platynus languidus Horn, 1892:42 = *Platynus ovatulus* Bates, 1884 (NEW SYNONYMY). Lectotype male (MCZ) hereby designated; type locality southern Arizona, hereby restricted to Cochise Stronghold, Dragoon Mtns., Cochise Co., AZ. Label data: Ari; Lectotype 2888 (red label); P. languidus Horn; Lectotype, Platynus languidus Horn, J. K. Liebherr 1990.

Note: Liebherr (1986:177) erroneously considered this species a member of the *Agonum nigriceps* species group. *Platynus ovatulus* is a member of the *P. ovatulus* species group, distributed in Mexico, Central America, and the Greater Antilles.

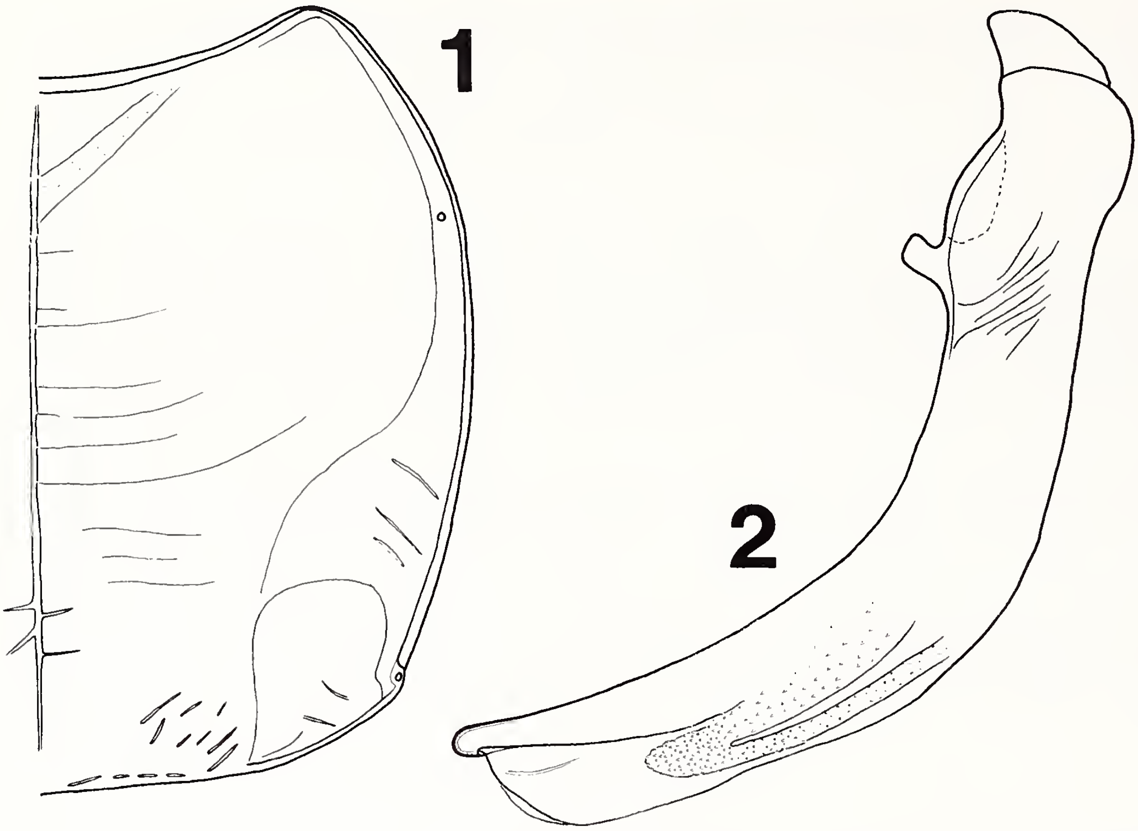
Platynus foveiceps Notman, 1919:233 = *Agonum fossigerum* Dejean, 1828 (NEW SYNONYMY). Holotype female (NMNH). Label data: Franktown, Nevada.

Agonum imitans (Notman)

Platynus imitans Notman, 1919:232.
Agonum (*Agonum*) *imitans,* Csiki, 1931:842.

Diagnosis. Third antennomere glabrous except for apical setae; head not impressed dorsally behind eyes; pronotum quadrate with broadly ovoid laterobasal depressions, laterobasal margin distinct inside evident hind angles (Fig. 1); elytral striae strongly punctate in basal half, smooth apically; elytra with three dorsal setae in third interval; elytral microsculpture of transverse lines intermittently joined into a transverse mesh; basal metatarsomeres with weak external and intermittent internal dorsal sulci; ungues with long ventral setae; body and leg color brunneous to piceous.

Description. Head moderately slender, eyes moderately convex. Mentum with broadly rounded unidentate median tooth, lateral depressions shallow. Basal 3 antennomeres glabrous except for apical setae; scape flavous to rufotestaceous, outer antennomeres with faint smoky cast. Pronotum quadrate with evident hind angles (Fig. 1); basal margin distinct inside basal setae; laterobasal depressions broad, ovoid, with strong isodiametric microsculpture in center; median base with weak longitudinal wrinkles, unmargined; median longitudinal impression fine; anterior transverse impressions shallow, broad, delimiting slightly depressed mediofrontal area of disc; front angles tightly rounded; lateral depressions of equal, moderate width from angle to slightly posterad lateral setae, then gradually widening to meet laterobasal depressions. Elytra with flattened disc; humeral angle very slightly angulate; elytral striae distinctly punctate basally, punctures becoming finer near middle of length, and absent in apical ⅓; elytral intervals convex throughout length; 3 dorsal setae in third interval; 15 setae in eighth interval; elytral microsculpture of transverse lines intermittently joined in a transverse mesh, the surface faintly iridescent. Metepisternum elongate, flight wings with reflexed apex, apparently fully developed. Legs moderately robust; mesocoxae with 2 ridge setae; metacoxae trisetose, inner seta present; mesofemur with 3 anteroventral setae; basal metatarsomere flattened dorsally, with weak external sulcus and indistinct internal sulcus; third metatarsomere with well-



Figs. 1, 2. *Agonum imitans* holotype. 1. Right half of pronotum, dorsal view. 2. Aedeagal median lobe, dorsal view, retracted position.

developed internal and external sulci and a median keel; apical tarsomeres of all legs with 3 pairs of long ventral setae.

Length. 6.9 mm.

Male genitalia. Parameres basally melanistic, mottled brunneous to piceous apically. Aedeagal median lobe nearly straight apically, evenly curved basally (Fig. 2); apex bluntly rounded; sagittal crest well developed; surface of shaft mostly smooth, faint wrinkles near basal bulb. Aedeagal internal sac unarmed, only uniformly faint spicules covering surface.

Type. Holotype male (NMNH). Type locality designated by Notman (1919) as "North America, locality uncertain." Label data: Type No. 104255 USNM (red label); Platynus imitans Type (blue label); Platynus rubripes (handwritten label).

Lindroth's (1966) key to *Agonum* in his expanded sense may be modified as follows to accommodate *A. imitans.*

62. 6.5–8.2 mm. Prothorax with suggested hind angles (Fig. 1 [also Lindroth 1966:607, Fig. 306m]). Elytral with ± piceous ground-color at least apically, quite unmetallic although slightly iridescent due to microsculpture 62a

62.′ Usually larger. Hind angles of prothorax almost lacking. Elytra black, almost constantly with metallic (often brilliant lustre) 63

62a. Elytral striae coarsely punctate in basal half, smooth apically. Elytral intervals convex, their microsculpture transverse mesh to rows of transverse lines ..*A. imitans*

62a′. Elytral striae with only traces of fine punctulae. Elytral intervals nearly flat, their microsculpture slightly transversely stretched isodiametric mesh ......*A. propinquum*

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DESCRIPTION OF A NEW SPECIES OF *PLACONOTUS* MACLEAY FROM KENYA, WITH NOTES ON THE MALE TERMINALIA OF OTHER AFRICAN SPECIES (COLEOPTERA: CUCUJIDAE (SENS. LAT.): LAEMOPHLOEINAE)

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Abstract.—*Placonotus embuensis,* n. sp., is described from Kenya. Illustrations of the habitus, male terminalia, and microsculpture are provided. Diagnostic structures of male terminalia of five additional African species of *Placonotus* [*P. bolivari* (Grouvelle), *P. decoratus* (Grouvelle), *P. donacioides* (Wollaston), *P. mestus* Lefkovitch, and *P. mossus* Lefkovitch] are also illustrated.

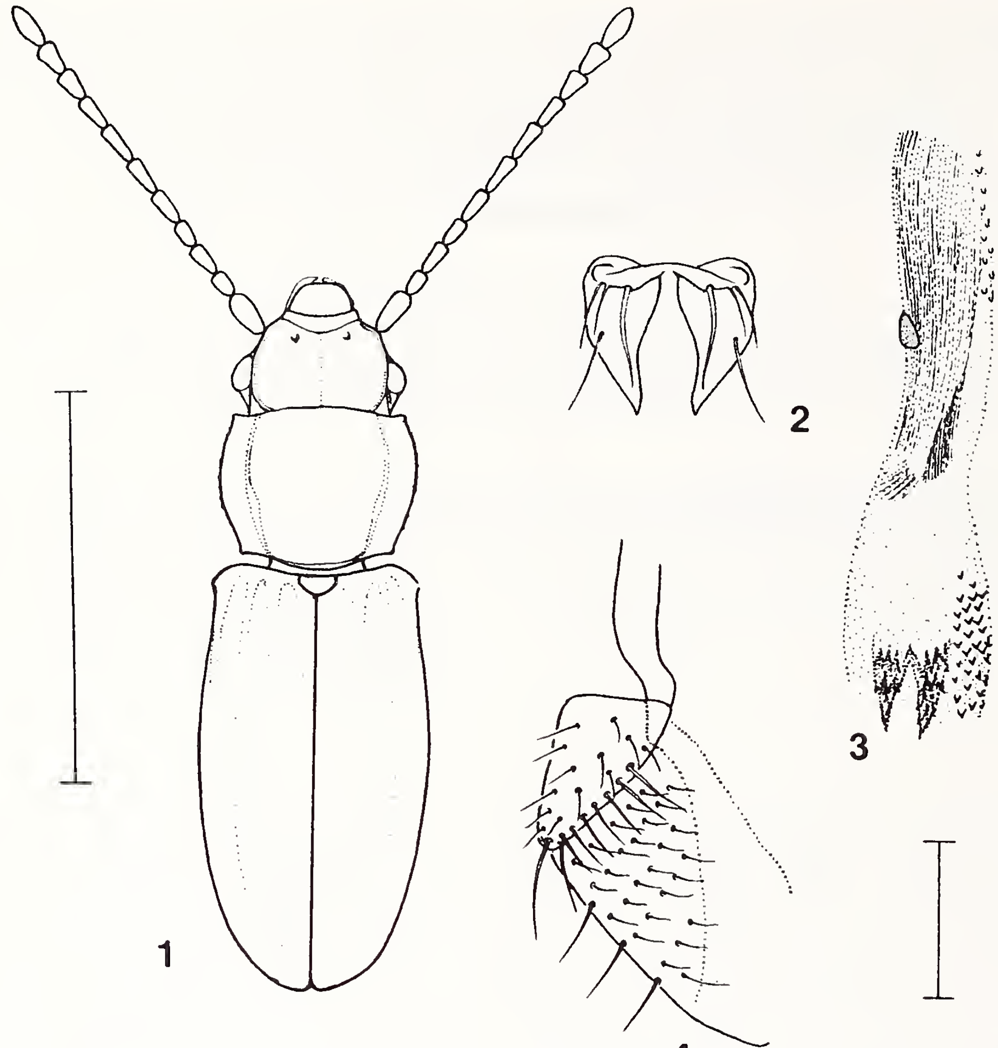
Lefkovitch (1962) listed 13 species of *Placonotus* MacLeay, including eight previously undescribed, from sub-Saharan Africa, Madeira, the Canaries, Madagascar, and the Seychelles. Lefkovitch (1965) recorded two of these from the Arabian peninsula. Slipinski (1984) added a third African species to the Arabian fauna and described a new species from Saudi Arabia that also may be found in eastern Africa. Thomas (1984) recorded two African species from the New World. These are apparently the only contemporary taxonomic references on the African species of *Placonotus.* Recently I discovered specimens of an undescribed African species in material from the Museum d'Histoire Naturelle, Geneva, which is described below.

Placonotus embuensis, new species
Figs. 1–6

Diagnosis. The combination of the following character states makes individuals of this species easily recognized in the African fauna: punctate, microreticulate dorsal surface of head and pronotum (Fig. 5); distinctive shape of the pronotum (Fig. 1); bituberculate frons in the male (Figs. 1, 6); and structure of the male genitalia and eighth abdominal segment, the combination of which I am calling the terminalia (Figs. 2–4).

Description. Form. Elongate, narrow; testaceous, legs and mouthparts paler. Length, 1.7 mm.

Head. Transverse, much broader across eyes than length from apex of epistome to base (1:1.8); lateral lines represented by ridge, associated groove more or less obscured by surface sculpture; frontoclypeal line represented by groove, more or less obscured laterally, distinct medially; mandibles not expanded laterally; punctures of disc larger in diameter than an eye facet, shallow, separated mostly by 2–3 diameters, each subtending a short, pale, inconspicuous seta; surface between punctures appearing matte due to microreticulation, more pronounced laterally than medially; a blunt tubercle located posterior to frontoclypeal line on each side about midway



Figs. 1–4. *Placonotus embuensis* Thomas. 1. Habitus of holotype male. 2. Parameres. 3. Sclerotization of internal sac. 4. Eighth abdominal segment, dorsal view. For Figure 1, line = 1.0 mm; for other figures line = 0.006 mm.

between median longitudinal line and antennal insertion; antennae elongate, filiform, attaining about basal third of elytra.

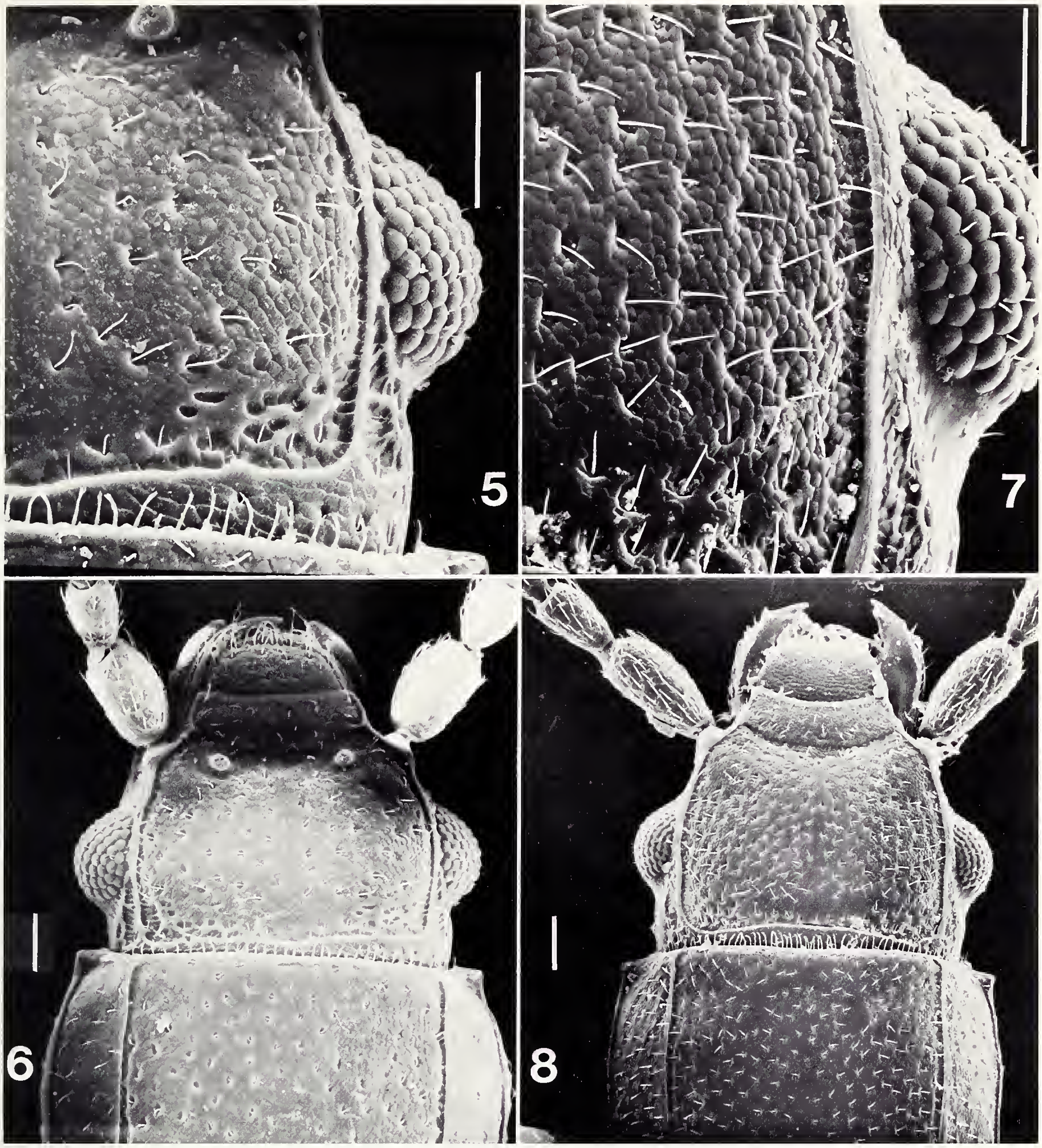
Pronotum. Transverse (1:1.3), distinctly rounded laterally, more so than usual for genus, broadest at about apical third; anterior angles obtuse, produced, slightly deflexed; posterior angles obtuse; sublateral lines as for genus; lateral margins minutely denticulate, especially posteriorly; punctation, sculpture, and pubescence as for head.

Elytra. Length : width ratio, 1.7:1; broadest just behind middle; conjointly rounded to apices, not subtruncate, exposing only tip of last visible abdominal segment; base of third elytral cell distinctly impressed, remainder of cells obsolescent, represented by longitudinal lines of shallow punctures; surface otherwise apparently impunctate, strongly microreticulate; pubescence consisting of scattered short, pale, inconspicuous setae.

Terminalia as in Figures 2–4.

Variation. The single male paratype is 1.6 mm in length; the two female paratypes are 1.9 mm and 2.0 mm in length. In the females, the antennae are proportionally shorter and the lateral margins of the pronotum less rounded.

Holotype. Male, in the Museum d'Histoire Naturelle, Geneva, with following data:



Figs. 5–8. SEM photographs of microsculpture of head and of head and pronotum of *Placonotus* spp. 5–6. *P. embuensis* Thomas. 7–8. *P. donacioides* (Wollaston). Line = 0.05 mm.

"KENYA Embu Irangi Forest St. 2000m. 11.X.77 MAHNERT PERRET" [terminalia dissected and glued to paper point with specimen].

Paratypes. Three, as follows: 1 male (gold sputter-coated for scanning electron microscopy), 2 females, all same data as holotype. The male paratype is deposited in the Florida State Collection of Arthropods, females in the Museum d'Histoire Naturelle.

DISCUSSION

Individuals of this species go to couplet 4 in Lefkovitch's key to the African species of *Placonotus* (Lefkovitch, 1962), where they do not agree with either alternative. In

their dull surface sheen (due to strong microreticulation) they are closest to *P. donacioides* (Wollaston) and *P. mossus* Lefkovitch. In the former, individuals are larger, the lateral margins of the pronotum are much less rounded (Fig. 8), the punctation of the dorsal surface denser (Fig. 7), and the male terminalia are much different (Figs. 10, 15, 17). Individuals of *P. mossus* lack dorsal punctation, have the lateral margins of the pronotum less rounded, and the male terminalia are different (Figs. 13, 14, 20). The frontal tubercles of male *P. embuensis* are unique among known species of *Placonotus*. The following replaces couplet 4 in the key to African species of *Placonotus*:

4. Dorsal surface of head and pronotum heavily microreticulate between punctures, so that surface appears dull .... *embuensis* Thomas
– Dorsal surface of head and pronotum not or slightly microreticulate; surface between punctures not dull 4a
4a. Smaller species (about 1.5–2 mm); pronotum distinctly transverse and head punctate; elytra 2.5–3.0 times as long as their combined width 5
– Larger species (about 1.8–2.3 mm); pronotum about as broad as long or if transverse, then head impunctate; elytra usually less than 2.5 times as long as their combined width 6

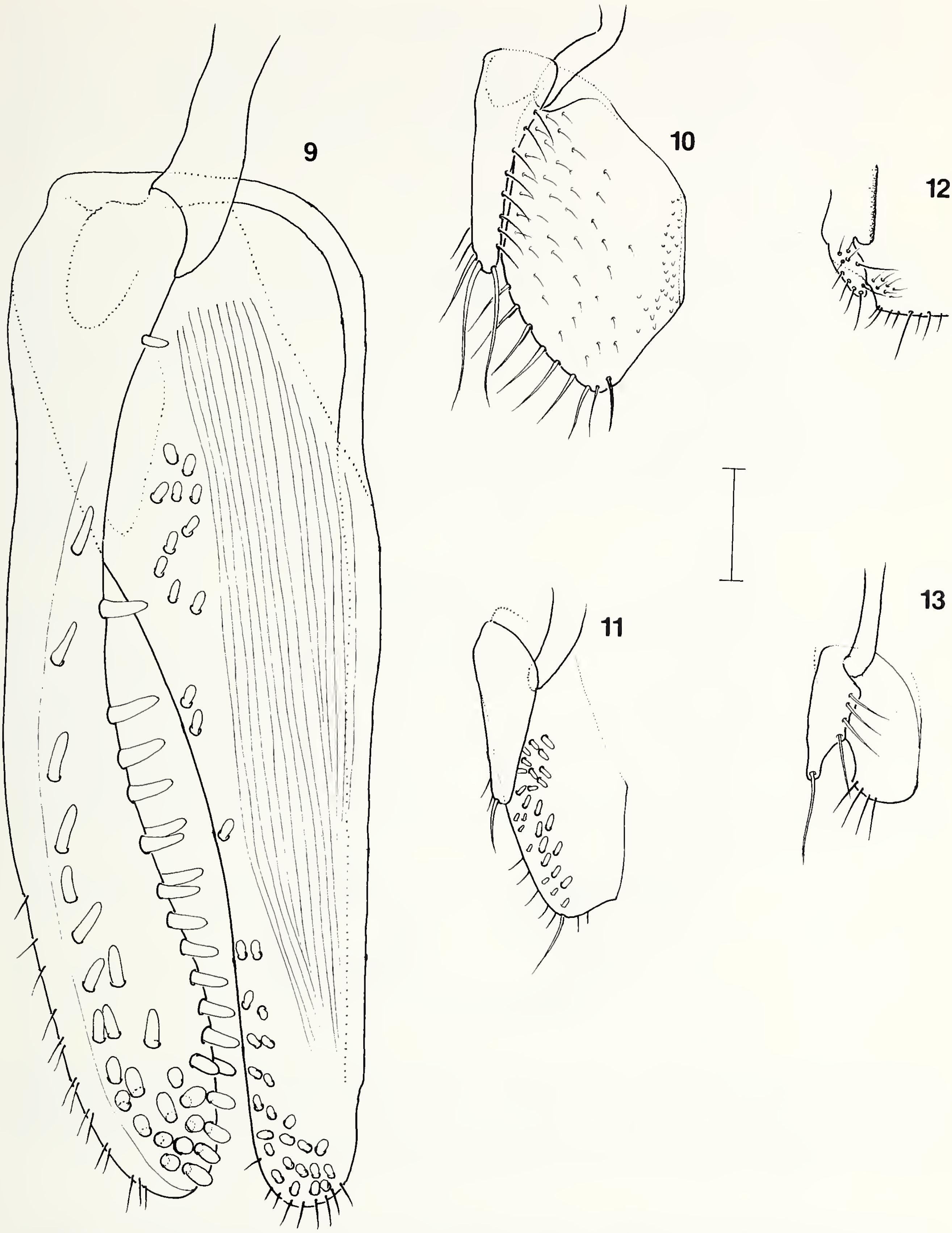
Although the terminalia offer excellent diagnostic characters, they have been little used to distinguish Old World species of *Placonotus*. Lefkovitch (1962) presented rather diagrammatic illustrations of the eighth abdominal segment, or claspers, of only two species, *P. subtruncatus* Lefkovitch and *P. africanus* Lefkovitch, and the entire terminalia of a third, *P. ealensis* Lefkovitch. These three species comprise Lefkovitch's *subtruncatus* species group, distinguished by their subtruncate elytra and separable only on characters of the male terminalia.

In addition to the claspers, the structure of the parameres, median lobe, and the armature of the internal sac are valuable taxonomically, although they require slide-mounting for proper examination. Thomas (1984) illustrated the parameres, ventral claspers, and internal sac of the two African species, *P. politissimus* and *P. majus*, occurring in the New World (in that publication, the captions on figs. 13 and 14 are reversed).

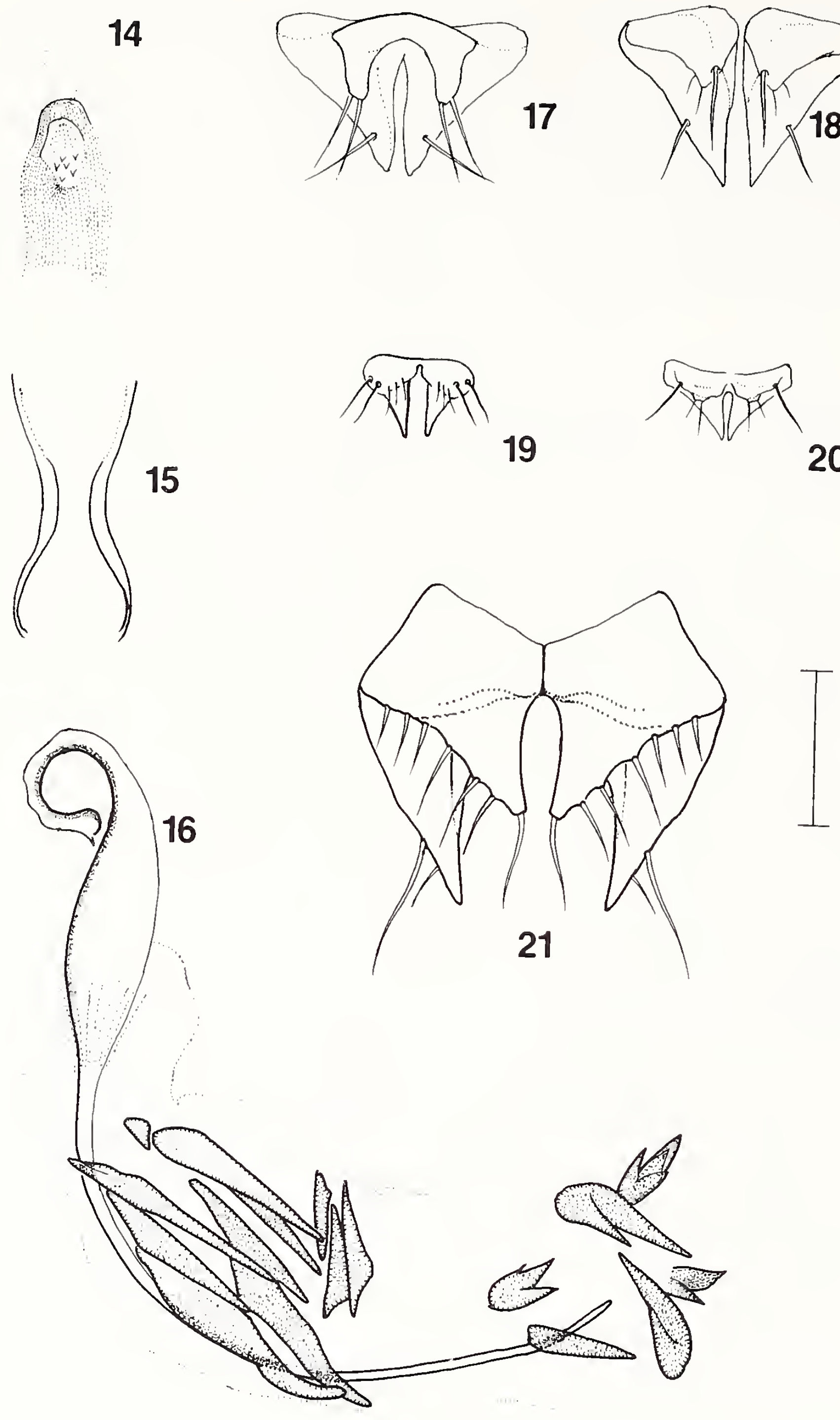
In addition to those of *P. embuensis*, diagnostic structures of the terminalia of five African species are presented here. Identification of specimens was based on the key in Lefkovitch (1962).

The structure of the claspers of *P. decoratus* (Fig. 9) suggests a close relationship with *P. africanus*; certainly both the claspers and the armature of the internal sac (Fig. 16) are similar to the corresponding structures found in the members of the New World *modestus* species group (see Thomas, 1984). A close relationship between *P. africanus* and the members of the *modestus* species group has been suggested previously (Thomas, 1984).

Based on the structures of the terminalia as illustrated by Lefkovitch (1962), the other two species of the *subtruncatus* group are not as similar to *P. africanus* as is *P. decoratus*, which also has subtruncate elytra. However, the parameres in *P. decoratus* (Fig. 21), and especially the ventral processes of the basal piece (Thomas, 1984), are also quite similar to those of *P. politissimus*, a species considered by Thomas (1984) to be of uncertain affinities.



Figs. 9–13. Eighth abdominal segment ("claspers") of *Placonotus* spp., dorsal view. 9. *P. decoratus* (Grouvelle). 10. *P. donaciodes* (Wollaston). 11. *P. bolivari* (Grouvelle). 12. *P. mestus* (Lefkovitch). 13. *P. mossus* Lefkovitch. Line = 0.006 mm.



Figs. 14–21. 14. Armature of internal sac, *P. mossus* Lefkovitch. 15. Same, *P. donacioides* (Wollaston). 16. Same, *P. decoratus* (Grouvelle). 17. Parameres of *P. donacioides* (Wollaston); 16. Same, *P. bolivari* (Grouvelle). 19. Same, *P. mestus* Lefkovitch. 20. Same, *P. mossus* Lefkovitch. 21. Same, *P. decoratus* (Grouvelle). Line = 0.006 mm.

The parameres and ventral processes (Fig. 13) of *P. bolivari* Grouvelle show some similarities with those of *P. decoratus* and *P. politissimus.* There are also some similarities in the claspers (Fig. 11), although in *P. bolivari* the ventral claspers lack peg setae. The two males of *P. bolivari* dissected did not have any armature of the internal sac; this would be a unique situation among known species of the genus. However, the armature of the internal sac may have been lost during dissection.

Although *P. donacioides* shares similar surface sculpture with *P. embuensis,* it is

very different in habitus (Fig. 8) and terminalia (Figs. 10, 15, 17). Individuals of *P. mossus* are distinctive in the African fauna due to their heavily microreticulate but impunctate dorsum. Their terminalia (Figs. 13, 14, 20), though, are similar to those of *P. mestus* Lefkovitch (Figs. 12, 19), especially the armature of the internal sac, which is here illustrated only for *P. mossus.*

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THE LARVA OF *BLEPHARIDATTA* (HYMENOPTERA: FORMICIDAE)

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Abstract.—The larva of the myrmicine genus *Blepharidatta* is described for the first time and illustrated. The genus is transferred from the tribe Ochetomyrmecini to a new tribe Blepharidattini.

HISTORY

Wheeler described the genus *Blepharidatta* in 1915 and assigned it to the myrmicine tribe Attini; he added, "but it differs so much from the other known genera in the structure of the head and especially the 2-jointed club of the antennae, the 4-toothed mandible and the regularly arranged setiform hairs on the dorsal surface, that it seems necessary to establish a distinct genus for its accommodation. Apart from the head the structure of the body is very simple and primitive for an Attiine [sic!] ant, even simpler and more primitive than in the genus Proatta, recently established by Forel for a unique Sumatran species." Wheeler also described as the type species *brasiliensis* from Pará, Brazil.

Gallardo (1916:319) reported finding several worker ants at Alta Gracia, a mountain resort ca. 20 mi south of Córdoba, which is in the province of Córdoba, in north-central Argentina.

Emery (1921–1922) placed *Blepharidatta* in the Dacetini (p. 12) because of its "tête cordiforme, échancrée par derrière et fort rétrecie devant" and separated it from the other genera (p. 313) by the "scrobe occupant tout le bord latéral de la tête; mandibules courtes, pouvant se croiser." He gave the distribution (p. 315–316) as "Brésil: Pará. Argentine" and said: "Cette Fourmis a une ressemblance frappante avec le genre fossile *Hypopomyrmex* de l'ambre de Sicile. M. Wheeler classe le genre *Blepharidatta* parmi les *Attini.* Il me semble avoir bien plus d'affinité avec les *Dacetini.*"

Wheeler stated (1922:376) that the habits of *Blepharidatta* are unknown. In his key to genera (p. 668) he separated *Blepharidatta* from all other attine genera by its distinct 2-jointed antennal club and its long antennal scrobes.

In 1953 Brown transferred *Blepharidatta* to the tribe Ochetomyrmecini because it is "very closely related to the species of *Wasmannia* Forel, differing chiefly in its more elongate head with produced posterior angles and in having a long, low petiolar node."

Kempf in 1967 described a second species (*B. conops*), from Três Lagoas, Mato Grosso State, Brazil. He also placed the genus in the tribe Ochetomyrmecini.

In 1975 Kempf devoted several pages to prove that *Ochetomyrmex* and *Wasmannia* could not be in the same tribe and suggested "at least as a provisional solution, the transfer of *Ochetomyrmex* to the Solenopsidine tribal complex, in the sense of

Ettershank. Thus the tribe name Ochetomyrmecini (nov. syn.) becomes meaningless, and the genera *Wasmannia* and *Blepharidatta* are without a tribal name. I refrain from coining a new name for these two groups, because it seems that the whole classification, generic and tribal, of the lower Myrmicinae needs urgent overhauling."

Our study of larvae supports the tribal separation of *Wasmannia* and *Ochetomyrmex* and the transfer of the latter to tribe Solenopsidini, but we are not about to join Kempf's refrain and put *Blepharidatta* and *Wasmannia* in the same tribe. We prefer to leave *Wasmannia* in Tribal Limbo, pending the Great Overhaul.

TRIBES

Before beginning the study of the larvae, we decided it would be advisable to get acquainted with the workers of the tribes involved. Characterizations of tribes are generally unsatisfactory, so we supported them by reality, namely examination of actual workers in our reference collection.

In his key (1922:655) Wheeler characterized the Dacetini thus: Clypeus prolonged between frontal carinae; head cordate, strongly narrowed in front, its dorsal corners not spinose. Antennae 4- to 12-jointed, the last joint being very much longer than the preceding; mandibles porrect.

We characterize the Proattini thus: Monotypic. Antennae 12-segmented, not clubbed. Head with an antennal scrobe, each dorsal corner produced into three tubercles. Dorsum with 10 spines on thorax and three on epinotum. Male with 13-segmented antennae and well developed pterostigma. Do not cultivate fungi. Old World (Malaysia).

We characterize *Wasmannia* thus: Monomorphic. Antennae 11-segmented, with 3-segmented club, with terminal segment decidedly predominant. Antennal scrobe shallow. Meso-epinotal suture impressed; surface of thorax roughened with sculpture only. Epinotum armed with spines. Hairs long and sparse.

We characterize the adults of tribe Attini as follows: Workers and female: antennae 11-segmented, without a club. Pterostigma narrow or absent. Worker: monomorphic or polymorphic. Head with antennal scrobe. Thoracic dorsum with spines, teeth, bosses or prominent ridges. Male: Antennae usually 13-segmented. Cultivate fungi. New World.

We establish a new tribe for *Blepharidatta* with the name Blepharidattini based on worker characters: Monotypic. Monomorphic. Head with deep antennal scrobes extending to dorsal corners. Each dorsal corner of head with an angulate tubercle. Eyes notably protuberant. Antennae 11-segmented, with a 2-segmented club. Mandibles triangular and 4-toothed, directed ventrally. Thoracic dorsum without impressed sutures; surface roughened with sculpture only. Epinotal spines long. Petiole long and with only a small node or none. Postpetiole small. Hairs sparse, long and bristle-like.

It is difficult to compare a single genus with 11 genera of Attini, but it is possible to compare *Blepharidatta* with the most primitive attine genus, *Cyphomyrmex*. In order to facilitate a multiple comparison we prepared a table (see Table 1) of 18 characters of *Blepharidatta, Cyphomyrmex* and *Wasmannia*. Characters 1–5 are shared by all three genera; 6 and 7 are shared by *Wasmannia* and *Blepharidatta*; 8–10 are shared by *Blepharidatta* and *Cyphomyrmex*; 11 and 12 are shared by *Wasmannia* and *Cyphomyrmex*; while 13–18 are different in each genus.

Table 1. Comparison of 18 characters of workers of *Blepheridatta, Cyphomyrmex* and *Wasmannia.*

Character	*Wasmannia*	*Blepharidatta*	*Cyphomyrmex*
1. Castes	monomorphic	monomorphic	monomorphic
2. Mandible	triangular	triangular	triangular
3. Mandibular teeth	4 subequal	4 subequal	4 subequal
4. Eyes	moderately large and protruding	moderately large and protruding	moderately large and protruding
5. Antennal segments	11	11	11
6. Epinotal spines	present	present	none
7. Humeral angles	dentiform	dentiform	rounded
8. Frontal carinae	not lobulate below	lobulate below	lobulate below
9. Scrobe	shallow	deep	deep
10. Sting	well developed	vestigial	vestigial
11. Dorsal corners of head	rounded	angularly tuberculate	rounded
12. Mesoepinotal suture	present	absent	present
13. Antennal club	3-segmented	2-segmented	no club
14. Petiole	large; node high, narrow	long; low node present or absent	short, low, wide
15. Postpetiole	normal	small	large
16. Gaster	1st somite long, others small	small	small, 1st somite covers others
17. Body hairs	long, erect, sparse	long, bristly, erect on dorsum	appressed, rather scale-like
18. Thoracic sculpture	rugae only	rugae and punctures	bosses or carinae

To us, this means that *Blepharidatta* should be placed in a monotypic tribe, if only adult anatomy is considered. However, taxonomists now maintain that a species should be defined by *all* its characters.

LARVAE

In September 1989 we received from Dr. J. Lattke in Caracas, Venezuela a most welcome gift of 2 workers and 12 larvae of *B. brasiliensis.* These not only enabled us to examine a very rare ant species but to describe a larva new to us and perhaps to shed some light on the tribal problem.

Blepharidatta brasiliensis Wheeler
Fig. 1

Length (through spiracles) 1.5–2 mm. Profile attoid; segmentation indistinct; spiracles on T2 0.01 mm in diameter, decreasing gradually to 0.008 mm on AI, and to 0.006 mm on AVIII. Integument minutely spinulose, the spinules more numerous

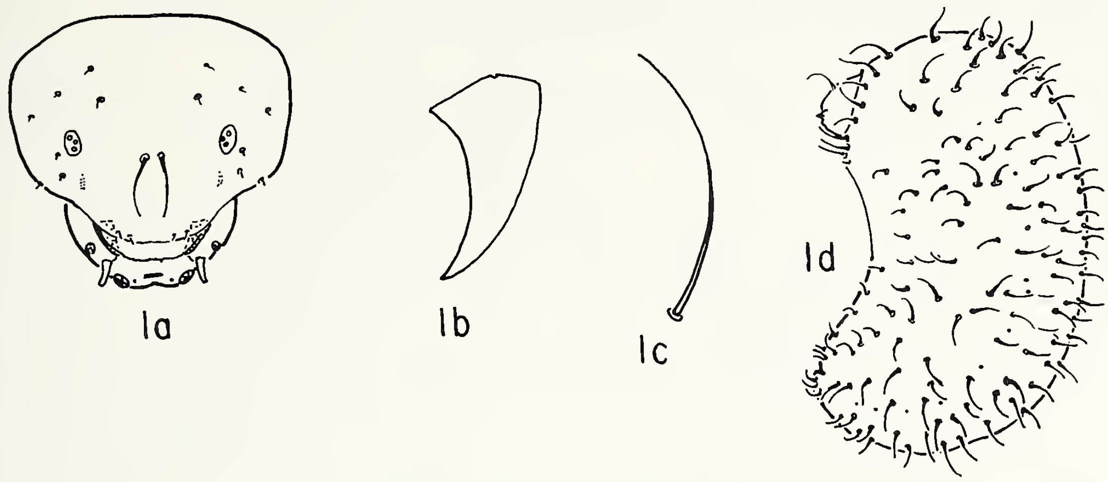


Fig. 1. *Blepharidatta brasiliensis.* a, Head in anterior view, ×100; b, left mandible in anterior view, ×625; c, body hair, ×100; d, larva in side view, ×30.

and in short rows on venter of anterior somites and dorsum of posterior somites. Body hairs sparse, 0.025–0.125 mm long, slightly curved, tip sometimes flexuous. Cranium suboctagonal, widest dorsally; integument of dorsal portion spinulose, the spinules minute and in short to long rows. Antennae large, at midlength of cranium, each with 3 sensilla, each of which bears a spinule. Head hairs few (ca. 22), very short (0.003–0.008 mm long), except for 2 near midline (ca. 0.06 mm long). Labrum crescentic, wide and very short, anterior surface with 2 sensilla; ventral surface with 6 sensilla; posterior surface with numerous rows of minute spinules. Mandible small, narrowly subtriangular; apex moderately sclerotized, sharp-pointed and without medial or superficial teeth. Maxilla with rounded apex (adnate?); palp a short frustum with 5 (4 apical and 1 lateral) sensilla; galea tall digitiform with 2 apical sensilla. Labium feebly bilobed, with short arcuate rows of minute spinules; palp an irregular projection with 5 sensilla; an isolated sensillum between each palp and the opening of the sericteries; the latter a transverse slit. Hypopharynx spinulose, the spinules minute and in arcuate rows, which are in subtransverse rows. (Material studied: 12 larvae from Alto Rio Mabaca, Amazonas, Venezuela, 2°1′N, 65°7′W, alt. 200 m, courtesy of J. Lattke.)

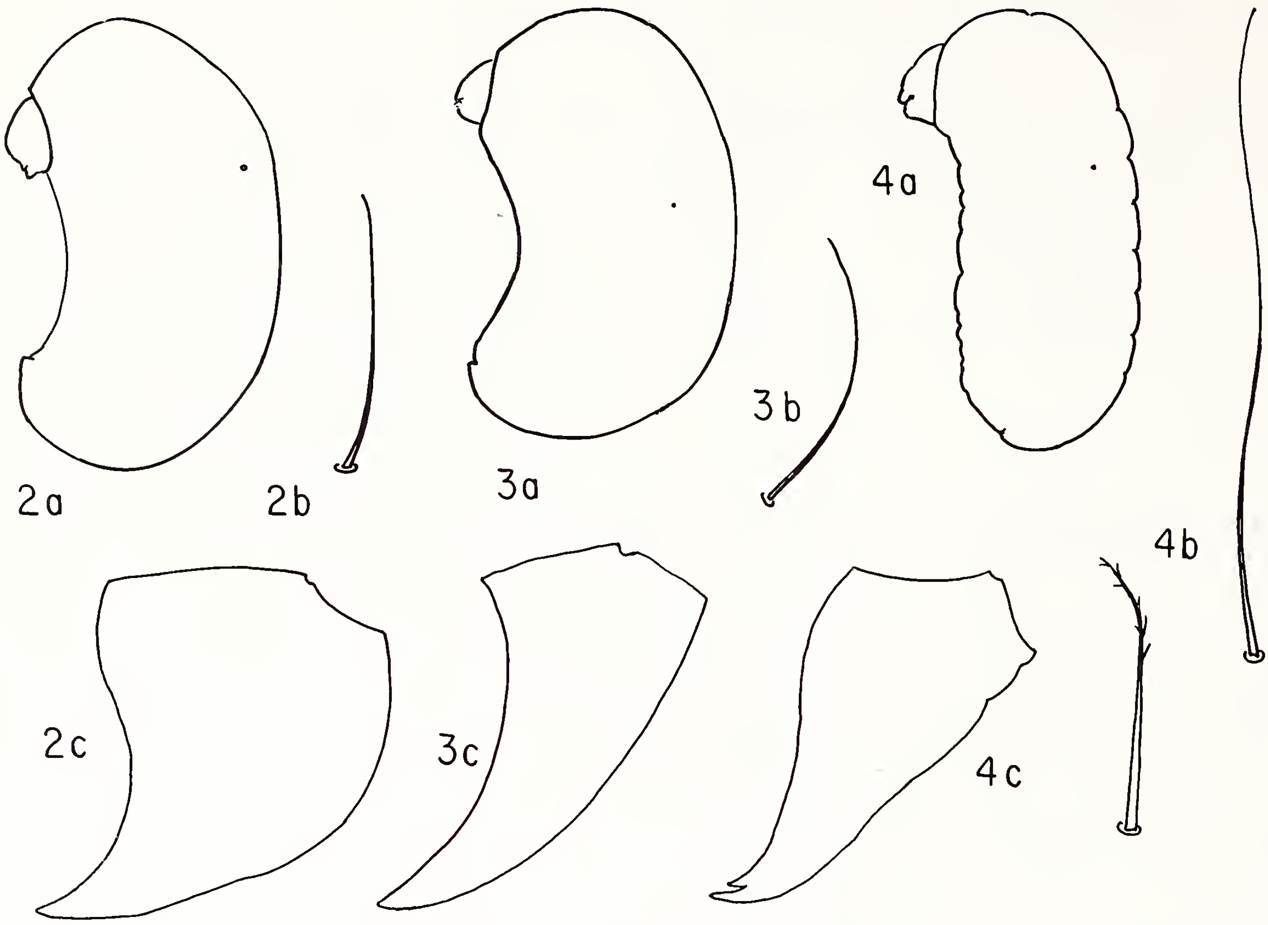
We have characterized the larvae of Attini (1976:60 and 1986:691) as follows: Profile attoid. Body almost naked, the few hairs minute to short and largely restricted to the ventral surface. Mandibles attoid, surface covered with coarse spinules, which are directed apically.

The larvae of several genera do not conform (see G. C. Wheeler, 1948), but they are kept in the Attini because their adults culture fungi. *Myrmicocrypta* has none of the distinctive larval characters, but it has adult characters. *Apterostigma* and *Sericomyrmex* have non-attoid mandibles, but adults and all other larval characters conform.

We characterized the larva of *Proatta* in 1985, but we now characterize it thus: Profile pheidoloid. Mandibles amblyoponoid, without spinules. Body hairs sparse, generally distributed, short, with tip curved or bifid.

We characterize the larva of *Wasmannia* thus: Profile pheidoloid. Body hairs sparse; short and denticulate and long unbranched. Mandibles pristomyrmecoid.

We characterize the larva of Blepharidattini thus: Profile attoid. Mandibles am-



Figs. 2–4. Comparison of larvae of *Cyphomyrmex, Blepharidatta* and *Wasmannia*. 2. *Cyphomyrmex*. a, Profile; b, body hair; c, left mandible in anterior view. 3. *Blepharidatta*. a, Profile; b, body hair; c, left mandible in anterior view. 4. *Wasmannia*. a, Profile; b, 2 types of body hairs; c, left mandible in anterior view.

blyoponoid, with two acute teeth, one apical and one subapical. Body hairs sparse and moderately long; generally distributed; unbranched, smooth and slightly curved.

In Figures 2–4 we compare the larva of a primitive attine (*Cyphomyrmex*), with that of *Wasmannia*, and with that of *Blepharidatta*.

CONCLUSION

Our overall conclusion is that the tribe Attini comprises the 11 fungus-growing genera. The genus *Proatta* remains in the monotypic tribe Proattini. The tribe Ochetomyrmecini is dissolved and the genus *Blepharidatta* is transferred to a new monotypic tribe Blepharidattini.

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ANOCHETUS BREVIDENTATUS, NEW SPECIES, A SECOND FOSSIL ODONTOMACHITI ANT (HYMENOPTERA: FORMICIDAE)

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Abstract.—I describe the new species *Anochetus brevidentatus* from Dominican Republic amber, possibly deposited 30–40 million years before present. This species is a member of the *emarginatus* species group and the *haytianus* superspecies. It is closely related to the extant *A. kempfi.* I present characters for distinguishing this ant from the others in the *haytianus* superspecies.

Recently we have seen a rapid growth of knowledge of ants of the Dominican Republic amber, due primarily to the work of Baroni-Urbani and Wilson (see Wilson, 1988 for references). One of these new species, *Anochetus corayi,* was recently described by Baroni-Urbani (1980). In this paper, I describe a second species in the genus *Anochetus* from Dominican amber.

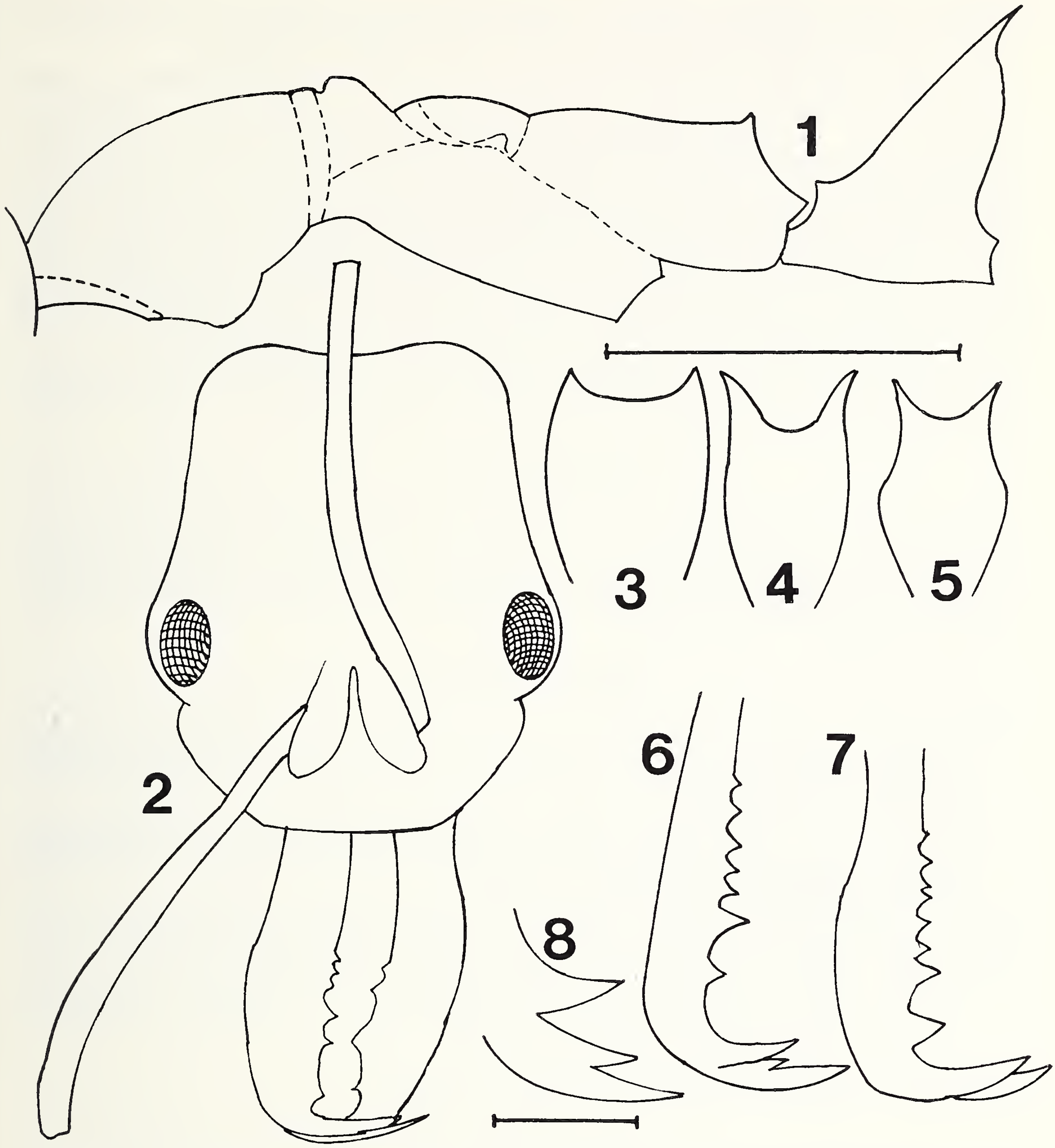
Anochetus brevidentatus, new species
Figs. 1, 2, 3, 8

Diagnosis. This species is closely related to *A. kempfi.* It differs in that the mandibular teeth are smaller (Figs. 2 and 6), the teeth on the petiolar node are much smaller (Figs. 3 and 4), the mandibles are enlarged in the middle (as in *A. haytianus*—Fig. 7) and it is smaller than *A. kempfi.* It can be easily distinguished from *A. haytianus* and *A. longispina* as the teeth on the node of the petiole are much smaller (Figs. 3 and 5) and it has teeth on the propodeum, which are absent on the latter species.

Description of worker: HL 1.34, HW 1.20, SL 1.40, ML 0.90, EL 0.2, WL 2.08 (abbreviations as in Brown, 1978, measurements in mm). Mandibles with three apical teeth (Fig. 8) in addition to six smaller teeth along mesial border (Fig. 2), mandible slightly thickened at one half length of mandible; eye appears to be relatively small (not easily seen in specimen); mesosoma similar to that of *A. kempfi,* anterior edge of mesonotum higher than level of pronotum; propodeum with pair of well developed spines, directed vertically (Fig. 1); anterior face of petiole almost flat (in profile), posterior face convex, node bidentate, teeth relatively small (Fig. 3). Erect hairs sparse, present on mandibles, dorsum of head, pronotum and gaster. Sculpture fine, parallel striae on most of mesosoma; gaster smooth and shining.

Female and male: Unknown.

Discussion. This species is a member of the *emarginatus* species group, defined by Brown (1978) as species of large size and slender build, mandibles serially dentate, and petiole bidentate. It shows some affinities with the *inermis* group of the genus, as it has relatively small eyes, teeth on the node, and the denticular configeration is



Figs. 1–8. *Anochetus* spp. workers. 1. *A. brevidentatus,* mesosoma and petiole. 2. *A. brevidentatus,* full face view of head. 3. *A. brevidentatus,* anterior face of petiole. 4. *A. kempfi,* anterior face of petiole. 5. *A. haytianus,* anterior face of petiole. 6. *A. kempfi,* right mandible. 7. *A. haytianus,* right mandible. 8. *A. brevidentatus,* apical mandibular teeth (from below). (Scale: Figs. 1–7 line equals 1 mm, Fig. 8 line equals 0.25 mm.)

similar to species in this group. The mesonotal outline is also similar to species in the *inermis* group. It is smaller than other species in the *emarginatus* group and could be identified as a member of the *inermis* group using Brown's key (1978). It is a member of the *haytianus* superspecies, defined as those species with six–nine teeth and denticles on the medial border of the mandible. This superspecies is found only in the West Indies, and includes *A. haytianus, A. kempfi, A. longispina* and *A. brev-*

identatus. The *emarginatus* and *mayri* species groups (to which the fossil species *A. corayi* belongs) are both represented in the recent fauna of Hispaniola.

Type series. Single holotype worker from the DOMINICAN REPUBLIC, La Toca Mine near Las Aguitas, imbedded in amber, which I purchased from Amberica S. A., Calle Z, No. 5 (NACO), P.O. Box 429-2, Santo Domingo, Dominican Republic. It is deposited in the Museum of Comparative Zoology, Harvard. The specimen is well preserved, in a clear brown amber matrix. The left mandible is somewhat twisted and the right antenna is missing the funiculus. Known only from the holotype. This amber is of the oldest and hardest in the Dominican Republic, and reported to be 30 to 40 million years old (Lambert et al., 1985). The age of this specimen is based on the presumed rate of methyl radical decay and may be questionable.

Etymology. From Latin, referring to the short teeth on the petiolar node, a character which separates it from all others in the superspecies *haytianus.*

ACKNOWLEDGMENTS

Dr. David Smith of the Systematic Entomological Laboratory, Agricultural Research Service, Washington, D.C., loaned specimens of *A. kempfi* and *A. haytianus.* John Lattke and two anonymous reviewers critically reviewed the manuscript. The two reviewers provided important information regarding the presumed age of the specimen.

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A REVISION OF THE FIRE ANTS, *SOLENOPSIS GEMINATA* GROUP (HYMENOPTERA: FORMICIDAE: MYRMICINAE)

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Abstract.—The subgenera and satellite genera of *Solenopsis* are reviewed. Synonymy under *Solenopsis* of all subgenera and of the genera *Bisolenopsis, Synsolenopsis, Paranamyrma,* and *Labauchena* is confirmed. Certain placement of the genus *Lilidris,* known from a single alate female, will require study of additional material, but *Lilidris* appears to be distinct from *Solenopsis.* The fire ants and their close relatives, *S. substituta* and *S. tridens,* are collectively designated as the *S. geminata* species group, which together with the parasitic *S. daguerrei* group (*Labauchena*) form a monophyletic lineage. *S. virulens,* a species phenetically similar to minors of *S. saevissima,* is also included in this revision, though it probably does not belong in the *S. geminata* group. Four native species, 2 introduced species, and 2 hybrid forms occur in North America. Seventeen species are known from South America. A key to major workers and illustrations of all species are included. Notes on the identification of queens are provided where these are sufficiently distinctive. The native North American species are *S. aurea* Wheeler, *S. amblychila* Wheeler **new status**, *S. geminata* (Fabricius), and *S. xyloni* (MacCook), and the introduced species are *S. invicta* Buren and *S. richteri* Forel from South America. *S. xyloni* × *geminata* and *S. invicta* × *richteri* are the hybrid forms. *S. invicta* × *richteri* is abundant and highly fertile in parts of Alabama, Mississippi and northwestern Georgia in North America, but this hybrid has not been observed in South America, even though the parent species have overlapping distributions in at least Santa Fé Province, Argentina. In South America, only *S. bruesi* Creighton **new status**, *S. gayi* (Spinola), *S. geminata* and *S. weyrauchi* **new species** occur in or to the west of the Andes. The latter is unusual in that it occurs at elevations up to 3,500 m or higher in the Peruvian Andes. To the east of the Andes are found *S. electra* Forel **new status**, *S. geminata, S. interrupta* Santschi, *S. invicta, S. macdonaghi* Santschi **new status**, *S. megergates* **new species**, *S. pusillignis* **new species**, *S. pythia* Santschi, *S. quinquecuspis* Forel, *S. richteri, S. saevissima* F. Smith, *S. substituta* Santschi **new status**, and *S. tridens* Forel. With the exception of *S. geminata, S. saevissima,* and *S. invicta* (at least part of whose geographic range is in the rain forest region) most of the South American species are endemic to the monsoon tropics or warm temperate regions of the southern part of the continent. *S. virulens* (F. Smith) **new status**, probably not a member of the *S. geminata* group but superficially resembling them, inhabits the forests of Amazonia.

"Fire ant" is the English name used by entomologists and many laymen for a group of formicid species traditionally placed in the subgenus *Solenopsis* (*Solenopsis*). In my experience, most English-speaking non-entomologists simply call them "red ants," and the equivalent "*hormiga colorada*" is a prevalent name for them in some Spanish-speaking parts of Central and South America. Other names include "*hormiga brava*" (fierce ant) in Spanish, and "*formiga de fogo*" (fire ant), "*formiga lava-pê*"

(wash-foot ant, referring to what one might do to remove the stinging insects after stepping into a mound) and "*formiga toicinheira*" (lard ant) in Portuguese. Undoubtedly, *S. geminata* has acquired many vernacular names where it has become established in tropical Africa, Asia and Polynesia.

Certain fire ants, particularly *S. invicta,* are considered serious pests in the southeastern United States. In areas of human habitat modification, fire ants may form dense populations. They build conspicuous earthen mounds, which are aggressively defended by the painful stinging of often great numbers of workers. *S. invicta* and its relatives have similar habits in much of South America, but they are apparently viewed as no more than minor pests there. This is probably more indicative of a generally lower tolerance of the presence of insects among North Americans than of a real difference in impact of the ants.

The concern about fire ants has created recognition of the need for a thorough revision of the fire ants, which is the purpose of this paper. Since Creighton's (1930) revision of *Solenopsis,* there has been no attempt to revise the subgenus *Solenopsis,* nor even to define it. More recent revisionary works are those of Wilson (1952), Snelling (1963) and Buren (1972). In these papers, coverage was limited to only a few species, and the authors (and Creighton, for most taxa) did not examine type specimens of the *Solenopsis* taxa described by Forel and Santschi, who described most of the named forms in the group. For this study, I have had the opportunity to study at least part of the syntype series of most taxa, those of *S. pylades, S. interrupta* and of some of the synonyms of *S. geminata* being the exceptions. Types of the former two were examined by W. F. Buren in 1974, and I have made use of his notes in my assessment of these taxa. Also, I have on loan from USNM a series of *S. interrupta* with the same collection data as the type series, which I believe to be workers from the same colony. Barry Bolton (BMNH) has examined types of the taxa synonymized with *S. geminata* in this paper described by Frederick Smith, and I accept his judgement that they do not differ specifically from *S. geminata.*

METHODS AND TERMINOLOGY

Recognition of major workers

This revision is based primarily on the major workers of fire ants, for it is generally in this subcaste that species-specific characteristics are best expressed. It is thus appropriate here that I discuss the term "major worker." In an attempt to arrive at a definition of the term, I made plots of maximum head width vs. head length of workers of all sizes for several fire ant species, pooling conspecific specimens from various colonies and localities. The resulting plots are weakly diphasic, i.e., showing a slightly different slope in the upper portion (Wilson, 1971, p. 141). One might call any worker falling within the upper phase of such a plot a major. Those experienced with fire ants in the field (Tschinkel, 1988a; Wojcik, unpubl.) note that the major workers of less populous colonies are not as large as those of very large colonies, but are clearly recognizable as major workers, especially by their characteristic head shape. On the other hand, worker populations from polygyne colonies or very young colonies do not, on casual observation contain any readily recognizable major workers (but see Tschinkel, 1988a), yet the largest workers of such populations may work out in the key. Thus, while "major worker" cannot be defined in absolute size terms,

for purposes of this paper, major workers may be loosely defined as the upper ⅓ to ¼ of the worker size distribution for most colonies.

Characters and possible pitfalls

Characters used for describing and identifying fire ants are of the sort commonly used in ant taxonomy. Some traditional characters, such as pilosity and surface sculpture patterns, are of limited use in fire ants because of the great homogeneity in these features across species in the group. The most useful characters are major worker head shape and color pattern. These and some other characters are discussed below.

Head shape of minor workers, males, and queens is nearly uniform throughout the fire ants. However, the head shape of major workers is often diagnostic. The difference in shape between heads of closely related species may be subtle, so I have made every attempt to carefully illustrate the typical head shape, and to provide metric clues to recognizing it. The user of this revision should be aware that not every specimen examined will look "typical," so that some isolated specimens will not be identifiable by this suite of characters.

It is virtually traditional in ant taxonomy to warn readers of the dangers of over-reliance on color as a means for identifying ants, and color variation in some fire ant species can be vexing, especially since it may alter the superficial appearance of other characteristics. Morphological analysis by a color neutral method such as scanning electron microscopy might do much to avoid this problem. Much local and regional color variation, superimposed on broader clinal patterns, is characteristic in the species *S. saevissima, S. invicta, S. geminata* and *S. xyloni,* all abundant and widely distributed species. It may then seem contradictory that color patterns of the remaining, less widely distributed species provide generally reliable characters for species recognition, and they are of some utility even in the above-mentioned species. Thus, color is frequently used in the descriptions and key to species. The danger in this is not that the color characters are not useful, but that there is so much variation in interpretation of color terms. I have thus limited myself to using English color names. I have found the Munsell system of naming soil colors useful as a general model for naming ant colors, but have not followed it exactly. *All color descriptions are based on observations of specimens at 25× under bright incandescent illumination.* Keep in mind that smaller workers and occasional majors with aberrant color patterns will be difficult to identify by color.

It is expected that genetic and chemical characterization of fire ant species will help overcome the deficiencies of a taxonomy based upon strictly morphological features, though it is safe to predict that new and unforeseen difficulties will arise as these types of data accumulate. For example, we have at the moment no clear concept of the ecological or evolutionary significance of the variation in alkaloid components seen in fire ant worker venom by R. K. vander Meer and colleagues (USDA fire ant project, unpubl.). Their data leave considerable room for varying taxonomic interpretations. Genetic data on fire ant species being developed by K. G. Ross (Ross and Trager, 1991) seem to me inherently less susceptible to misinterpretation, but there is no doubt both sets of data will greatly enhance our general ability to further refine the taxonomy of these ants.

Geographical distribution is another characteristic that may help distinguish fire ant species, but one must exercise some caution in its use, since fire ant species are readily transported to new localities where they may become established. The successful establishment of *S. invicta, S. richteri* and *S. geminata* in lands far from their native ranges is well known, but it appears that some disjunct populations of these and other species within South America may be the result of introductions.

Measurements

Measurements were made at 40× or 50× on a Nikon SMZ-10 or Wild M5 stereo dissecting microscope, respectively. *For polymorphic species, approximate ranges (including absolute maxima) are reported only for workers with HL > 0.99 mm. For monomorphic species, the full known size range is given.* When a single individual of a species was notably larger than all others measured, or when specimens from a single locality averaged larger than the others measured, data for such specimens are reported in parentheses following the "normal" range. Measurements of holotypes of new species are listed separately. Abbreviations and definitions for these measurements and indices calculated from them (and other abbreviations used in the text) are given below. Other measurements and proportions, both for majors and for other castes are defined as necessary in the text. Measurements and indices:

HL—Head length; in full face view (defined below), the distance along the sagittal axis of the head between the anterior midpoint of the clypeus (exclusive of median clypeal tooth) and the posterior margin of the head or, if posterior margin concave, between the clypeal margin and a line tangent to the two most posterior points of the rear margin.

HW—Head width; in full face view, the maximum width of head behind the eyes.

SL—Scape length; length of shaft of antennal scape, exclusive of basal articulation.

EL—Eye length; maximum diameter of compound eye.

PW—Pronotum width; maximum width of pronotum in dorsal view.

AL—Thorax (alitrunk) length; distance from anterior base of pronotum (exclusive of anterior "cervical flange," which is often hidden from view) to posterior edge of metapleuron.

CI—Cephalic index; HW × 100/HL.

SI—Scape index; SL × 100/HW.

OI—Ocular index; EL × 100/HL.

Abbreviations for viewing orientations:

ffv—Full face view of the head, whereby which one obtains the greatest straight-line distance between the midpoints of the clypeal border and the vertex (posterior border). Viewing axis is approximately perpendicular to the surface of the frons.

lv—Profile or strict lateral view.

pdv—Posterodorsal view, useful for examination of some features of the thorax, and of the petiole and postpetiole.

Depositories of specimens:

AMNH—American Museum of Natural History, New York.
BMNH—British Museum (Natural History), London.
FSCA—Florida State Collection of Arthropods, Gainesville.
IML—Instituto Miguel Lillo, Tucumán, Argentina.
LACM—Los Angeles County Museum of Natural History.
MCZ—Museum of Comparative Zoology, Harvard University, Cambridge, MA.
MZSP—Museu de Zoologia, Universidade de São Paulo, Brazil.
USNM—United States National Museum, Washington, DC.

RESULTS

In this section, I first discuss classification within the genus *Solenopsis* and of some supposedly separate but closely related groups. I then characterize the fire ants in a general description of morphology of major workers, followed by brief summaries from the literature of other characteristics. A key to workers follows, and this is followed by accounts of the species complexes and subcomplexes and their contained species. Minor workers of most species are nearly or indeed indistinguishable. Males are poorly known and in most cases can reliably be sorted only to species complex, and are thus not keyed or described. The queens, while more readily distinguishable than males, are for many species poorly represented in collections, and in identifying them, one must usually rely on associated major workers. In a few cases where queens are the most morphologically distinctive caste, diagnostically useful queen characters are pointed out in the notes accompanying species descriptions.

Synonymic notes on the subgenera and satellite genera of *Solenopsis*

The subgenera of *Solenopsis,* and the related genera (sometimes considered subgenera) *Bisolenopsis, Synsolenopsis, Lilidris, Labauchena,* and *Paranamyrma* were synonymized into *Solenopsis* with little explanation by Ettershank (1966). Bolton (1987) presented arguments supporting these synonymies, especially that of the subgenus *Diplorhoptrum.* Ettershank recognized three "natural" groups in *Solenopsis*: the fire ants, the "small species," and the socially parasitic forms. Aside from the fire ants, which are a natural (though paraphyletic) species group, I believe the groupings in *Solenopsis* will sort out very differently from Ettershank's when the genus is subjected to phylogenetic analysis.

For example, there seem to be several lineages of "small species." Creighton (1930) grouped the subgenus *Diplorhoptrum* (here called the *S. fugax* group) into 5 species groups which may better account for the diversity within the "small species." The phylogeny of Creighton's (1930) 5 groups is unresolved, and the 5 species groups did not, furthermore, include all of the diversity represented by Ettershank's "small species." Additional groups of small *Solenopsis* not contained in the *S. fugax* group include the subgenera *Euophthalma, Granisolenopsis, Diagyne,* and *Oedaleocerus,* and the so-called genera *Bisolenopsis* and *Synsolenopsis.*

The distinctions between these taxa are anything but clearly defined, as the fol-

lowing examples will illustrate. (1) The single known species of *Granisolenopsis* seems to be a member of a South American complex of small *Solenopsis* species characterized by weakly polymorphic or dimorphic workers. Its major worker has head morphology convergently developed to resemble a minuscule *S. geminata,* and its queen has a narrow, permanently wingless thorax. Conditions approximating these are seen in some other small *Solenopsis* (all classified as *Diplorhoptrum*) from South America. (2) *S. globularia* (the type species of *Euophthalma*) and its varieties and subspecies are a group of small *Solenopsis* species which share several, apparently synapomorphic features with the *S. tenuis* complex of the *S. fugax* group and should be considered related to it. (3) *S. virulens* is treated along with the fire ants in this revision, but this is somewhat arbitrary, as the species has features suggesting relationship to *S. globularia* (see discussion of *S. virulens* for details). (4) On the other hand, a species described as a *Euophthalma, S. huachucana* is unmistakably a fire ant, namely the young queen and nanitic workers of *S. aurea.* (5) *Diagyne* has queens with distinctive mandibular dentition, but the workers are not distinguishable at the species-group level from the globularia-like *Euophthalma.* (6) The *Euophthalma* species outside of the *globularia*(*-tenuis*) group are apparently not differentiable from Kusnezov's (1957) genera *Bisolenopsis* and *Synsolenopsis.* The few specimens I have studied within these latter "genera" conform in some respects to my view of what ancestral *Solenopsis* may have looked like. They are markedly sculptured and sutured, have propodeal projections, relatively well-developed eyes, and flagellar segments of intermediate length between those of the fire ants and of the *S. fugax* group.

I also differ from Ettershank's classification by recognizing 2 distinct origins of workerless inquilinism in *Solenopsis,* namely "*Labauchena*" and "*Paranamyrma.*" Both show strong signs of phylogenetic ties to the species groups containing their hosts, suggesting a recent common ancestry.

It is clear that the genus-level taxa (including subgenera) in and around *Solenopsis* are largely meaningless and inseparable. I thus reaffirm Ettershank's synonymy of the free-living taxa *Bisolenopsis* and *Synsolenopsis,* and of the parasitic genera *Labauchena* and *Paranamyrma* under *Solenopsis.* And though there are a number of recognizable species groups in the genus, I agree with Ettershank (1966) and Bolton (1987) in not formally recognizing any of the above genera and subgenera, since none appear to be clear-cut monophyletic groups.

Lilidris, represented by a single queen described by Kusnezov (1958) may not, however, belong in *Solenopsis.* Its antenna, though 10-segmented, bears an apparently 3-segmented club. The wing venation of *Lilidris* is a little different from any known *Solenopsis,* but venation is variable in *Solenopsis,* and very likely will encompass that of *Lilidris* when studied in more species. The anterior metatarsal "brush" of *Lilidris* is also distinctive.

Based on the above, I refer henceforth to the fire ants and their close relatives, *S. substituta* and *S. tridens,* as the *S. geminata* group. Note that this group is informal and paraphyletic (or even polyphyletic, if *S. virulens* is included). A strictly monophyletic formal taxon containing the fire ants should also properly include the species in "*Labauchena.*" The latter are derived, with modifications typical of inquilinous ants, from ancestors that would be placed within the *saevissima* complex. Revision of these rarely collected inquilines is not attempted in this paper.

Within the *S. geminata* group, I refer to smaller groupings of related species as

species complexes, and at a still lower level, subcomplexes. These are briefly characterized at the beginning of the descriptions of their included species.

General description

A general morphological description of workers of the *S. geminata* group follows, provided to eliminate repetition of characteristics common to all species in the treatments of individual species, to provide a common basis for comparison, and for better understanding of the key and descriptions. A brief review from the literature of other characteristics of fire ants follows the morphological description.

Morphology

The description proceeds anterior to posterior. The orientation necessary for proper viewing is indicated in parentheses. Features of the minors are presented parenthetically, for comparison with the monomorphic workers of *S. virulens* and of the *S. tridens* complex.

Head (ffv) usually longer than broad, usually widest behind eyes; sides straight to weakly convex in species with quadrate or trapezoidal head shape, more convex in those with elliptical, ovate or cordate head shape (minor head shape elliptical, ovate or subrectangular, widest at or in front of eyes); posterior border weakly to notably concave, or less often with angular emargination (faintly concave to convex in minors); the concavity 1–2 × as wide as the distance between apices of frontal lobes; lower edge of distal border of clypeus bearing a large median seta, this usually borne on a projecting triangular tooth, the latter reduced or lost in some species; clypeal carinae divergent distad, usually projecting as isosceles-triangular teeth, these somewhat to notably larger than median tooth and always much larger than paracarinal teeth, which may be lacking (especially in smaller workers), carinal and paracarinal teeth more dorsad on clypeal border than median tooth; mandibles 4- or less often 3-toothed (teeth may be worn off in older specimens, but are always present at eclosion); mandible curved, distal portion of outer border usually at a weakly obtuse angle to basal portion (about 100°, angle larger in minors); mandibular costulae 6–10, complete throughout length of mandible or obsolete medially, sometimes bifurcate distally; eye (lv) ovate, elliptical or reniform, with from 45–100 facets (20–60 in minors); scapes (ffv) curved basally, thickest subapically; scape length significantly less to a little less than length between basal articulation of scape and most distant portion of posterior border, i.e., scape apex not surpassing posterior border of head (often as long or notably longer than this distance in minors and monomorphic species); anterodorsal pronotal border (pdv), weakly to notably convex; anterolateral pronotal corners variously developed, broadly rounded to distinctly angular and bearing obliquely or transversely oriented, "humeral bosses"; promesonotal suture chevron-shaped with a small dorsal projection at apex, or parabolic, or strongly convex, rarely obsolete, and this only in smaller majors (commonly so in minors); pronotum (lv) usually with steep anterior declivity set off from dorsum, pronotal dorsum forming an even convexity with mesonotal dorsum, or with a slight break in outline at point of anterior mesonotal projection; metanotal impression conspicuous, set off by steep, variously sculptured, posterior mesonotal and anterior propodeal declivities, the former declivity often higher than the latter (metanotal im-

pression shallower and less sculptured in minors); metanotal spiracles small, positioned dorsolaterally; propodeum (pdv) with dorsal face concave, descending through an even curve into declivous face; in profile (lv) propodeum usually appears angular because of longitudinal, posterolateral bosses or short rounded carinae (bosses lacking or weakly developed in minors so propodeal profile less or not at all angular); petiolar peduncle shorter than to slightly longer than base of node; profile of petiolar node cuneate or thick-squamose to globular, with anterior face straight to weakly convex and posterior face convex, the faces meeting through strongly convex dorsal portion; from behind outline of petiolar node (pdv) globular, subovate, or with more or less convex dorsal face meeting straight or weakly concave sides through rounded angles, sides convergent ventrad; profile (lv) of postpetiolar node in profile typically lower than that of petiole, appearing globular or nearly so, with a short posterior peduncle; from behind outline of postpetiolar node (pdv) globular to subtrapezoidal or subrectangular with dorsum convex (always more or less globular in minors); postpetiole varying from slightly to notably wider than petiole.

Integument mostly smooth; except for piligerous foveolae, and sculpture of mesometapleuron, propodeum, petiolar peduncle and rear face of postpetiole (sculpture always less developed in minors); diameter and sometimes shape of piligerous foveolae varying in diagnostically useful ways (small, round and inconspicuous in minors); sculpture of mesometapleuron consisting of longitudinal striae or rugae with varying levels of interstitial punctation; sculpture of propodeum and of postpetiole variable and often diagnostically useful at species level; declivous face of propodeum with weak transverse rugae or, more often, unsculptured on upper portion, on lower portion with concentric semicircular rugae continuous with those of metapleuron, but more widely spaced and usually lacking intersticial sculpture; petiolar peduncle usually faintly areolate or punctate, this sculpture continued posterad to base of node in some species; venter of petiole with longitudinal median carina and anteroventral process consisting of one to a few small teeth or a transparent flange, occasionally absent; dorsum of petiolar and postpetiolar nodes often weakly scalloped or longitudinally grooved; petiolar dorsum otherwise unsculptured; postpetiolar dorsum unsculptured or with sculpture resembling but weaker than that of postpetiolar posterior face; posterior face of postpetiole with varying, diagnostically useful combinations and distributions of transverse striae and punctation, especially on lower portion; sides of postpetiole usually striate-punctate; venter of postpetiole usually coarsely punctate with a few coarse longitudinal rugae.

Pilosity composed of yellowish or reddish brown setae, these normally more or less cylindrical and tapering distally, or more precisely, narrowly conical; longer setae curved; mesonotum usually with at least 20 erect setae (less in minors); mesopleuron with few aside from those on ventral edge; in most species pilosity varies greatly in length on a single specimen, longest hairs on thoracic dorsum usually at least 2.5× length of shortest; suberect pubescence present in a conspicuous patch on cervical flange of prothorax; less often, dilute, appressed pubescence often present on anterior face of petiolar node, and rarely some on propodeal dorsum.

Color ranging from nearly uniform honey-yellow to brownish black, in lighter shaded forms with at least posterior band of tergites usually notably darker; some species with more or less uniform color pattern in all samples; others spanning nearly the entire range for the species group, though typically not within a single colony;

(minor workers often darker and more uniformly colored than majors from the same colony).

Sting morphology

Kugler (1978) published an extensive review of the myrmicine sting apparatus, to which the reader should refer for details. Kugler's analysis resulted in *Solenopsis* genus group containing *Megalomyrmex, Monomorium* (including Chelaner), and *Oxyepoecus,* known relatives of *Solenopsis* (Ettershank, 1966; Bolton, 1987). Also included in this group by Kugler was a pair of *Rogeria* species. Their relationship to *Solenopsis* is contradicted by other lines of evidence.

Malpighian tubules

Brown (1988) surveyed Malpighian tubule numbers of ants. Among the above mentioned relatives of *Solenopsis,* 2 *Megalomyrmex* spp. (perhaps the most "primitive" genus in the group) had 5 Malpighian tubules, while all the remaining species (including 1 or 2 spp. from each of the other 3 genera had 4 tubules (a synapomorphy?). The tubules are not cryptonephric.

Larval morphology

Wheeler and Wheeler (1960a) divided what were then considered to be members of the tribe Solenopsidini into six genus groups. The genera *Solenopsis, Monomorium, Oxyepoecus,* and *Megalomyrmex,* (and *Anergates,* now thought to be a member of the Tetramoriini) are grouped in the solenopsidiform genera; those with short, stout, superficially straight body form (but with anterior ventral portion of thorax curved), ends rounded, neck very short or lacking, and anus ventral. Later the Wheelers (1960b) described the larvae of *S. picta, S. pergandei,* and *S. globularia littoralis* (which I consider to belong to 3 distinct species groups) as "similar to *S. geminata,*" differing in details of size and pilosity (confirming the close relationship of all *Solenopsis*).

Karyotypes

Taber and Cokendolpher (1988) reported the karyotypes of *S. xyloni* specimens from Texas and Arizona, synthesized their results with those from previous work, and listed all pertinent references. Karyotypes of the 2 *S. xyloni* populations were identical, and their chromosome morphology closely resembled that of *S. aurea, S. invicta* and *S. saevissima,* but differed from that of *S. geminata* and *S. richteri.* The diploid complement is 32 in all species, but as indicated by their results, chromosome morphology varies in ways that appear to be unrelated to taxonomic groupings within the *S. geminata* group.

Venom and cuticular hydrocarbon chemistry

Blum et al. (1985 and included references) have studied a variety of *Solenopsis* spp. and some in related genera. It appears that *Solenopsis* species exhibit a chemical synapomorphy of the presence of 2-alkyl-6-methylpiperidine alkaloids in the venom.

Furthermore, most species of *Solenopsis* and *Monomorium* contain another group of alkaloids, the 2,5-dialkyl-1-pyrrolines, alkaloids thus far unknown in any other ants. Alkyl side chain length and the proportions of components bearing different side chains vary within species, but in general, variation between species is much greater. The interspecific variation is already sufficiently characterized for some populations to be of taxonomic utility. Vander Meer and Lofgren (1988) recently demonstrated this for some *S. saevissima* complex species, and list most of the pertinent literature. Furthermore, they presented data on cuticular hydrocarbon variation and briefly discussed questions concerning species distinctions arising from the chemical studies. In a study by Ross et al. (1987), chemical and morphological phenotype, and genetic (allozymic) characters for recognizing *S. invicta, S. richteri,* and their hybrid in North America were shown to be highly correlated.

Allozymes

Ross (1988) discusses use of allozymes for studying systematic problems in complexes of closely related and cryptic species. Genetic characterization of fire ants was initiated by Ross and colleagues (Ross et al., 1987, and included references). Results of a study on the genetics of 6 Argentine taxa of the *S. saevissima* complex will be reported elsewhere (Ross and Trager, 1991). The morphological species concepts presented in this revision are for the most part strongly corroborated by our genetic data, though between 4 and 5% of the 200 samples studied bore such unique allozymes that they could not be placed with any of the larger genetic groupings.

Natural history

A huge body of literature has developed on the biology of fire ants (especially *S. invicta*), but a full accounting of the natural history of these ants is still lacking. Prominent papers on fire ant natural history are those by Tschinkel and coworkers (Tschinkel, 1986, 1988a, b; Porter and Tschinkel, 1988), Vinson and Sorensen (1986), Wojcik (1986), and Porter and Savignano (1990).

Colony foundation is effected by small groups of queens or single individuals following mating flights, which occur under conditions of low wind velocity, either at dusk following rain earlier in the day (*geminata* complex), or in late morning to mid-afternoon following rain the previous day or night (*saevissima* complex). The first brood of a dozen or less workers (more in pleometrotic efforts) is reared out in a month or so. Usually, only one queen survives the colony foundation period, the others being eliminated by the workers. In a year or so, the colony grows to many thousands of individuals. Newly colonized areas may have very high densities of colonies, but through territorial interactions, certain colonies eliminate most of their neighbors as they grow, so that densities in mature populations generally fall into the 30–100 nest/ha range.

Locally, mound densities may be much higher. This is associated with polygyne (multiple queen) colony populations, where densities may be as high as 1,000 mounds/ha, with densities of 300 mounds/ha not uncommon. These arise either by survival of co-foundresses or by adoption of newly mated queens, and are characterized by colonies with several to many hundreds of queens, diminished territoriality and small average worker size. This phenomenon is best known in the North American pop-

ulation of *S. invicta* (Lofgren and Williams, 1984), but I have made several collections from polygyne populations of *S. invicta, S. richteri,* and *S. quinquecuspis* in Argentina, and of *S. geminata* in Florida. Circumstantial evidence (small worker size, high mound density) points to the occurrence of polygyny in Argentine and Bolivian *S. interrupta* and Brazilian and Bolivian *S. invicta* as well, though conditions were not propitious for me to collect queens from these colonies. Most of the literature on polygyny in fire ants is cited in Glancey and Lofgren (1988) and in Porter and Savignano (1990).

The large workers spend relatively little time away from the nest, but come to the surface readily when the nest is disturbed. Major workers are also important for their food storage capacity, and often have the crop full of oily liquid. Small to medium-size workers forage along both surface and subterranean trails. Food sources are highly varied, but protein and fats from varied invertebrate prey or vertebrate carrion, and carbohydrates from fallen fruits, floral and extrafloral nectaries predominate in the diet of most fire ants. *S. geminata* is unusual in harvesting and milling a large number of seeds, but this behavior occurs in rudimentary fashion in all or most other species.

Fire ants recruit actively to large food sources, and tend to displace other ants from them. Some species of *Pheidole, Paratrechina* and other genera tend to find and recruit to such food items more quickly than fire ants, and may be able to carry off the food before fire ant workers are recruited. Once fire ants arrive in great numbers, they drive off other ants by lunging at them, or more often by wagging their gasters, sting exposed and bearing a droplet of venom, near the other ants. The latter are usually so repelled by the volatile components of the venom that they offer little resistance.

Nests are most often in moist sites, such as river banks, pond edges, swales and swampy areas, and their man made analogues, watered lawns and highway rights of way. In areas with argillaceous soils, a conical or domose mound up to a meter across and nearly as high may be a nearly permanent sign of the nest of species of the *saevissima* complex. When colonies die or move out, these mounds may be colonized by other colonies or nest-founding queens, including species of other genera. Occasionally, portions of active fire ant mounds may be occupied by other ants (e.g., *Acromyrmex* or *Paratrechina*) or by termites. In sandy areas, fire ant mounds collapse through disuse in dry, and especially in hot weather. In species inhabiting xeric areas mounds may be built up only during the peak mating flight period.

KEY TO MAJOR WORKERS OF *SOLENOPSIS* WESTWOOD; SPECIES OF THE *GEMINATA* GROUP (SENSU EMERY, 1925)

NOTE: This key is not designed for identification of minor workers. Workers of the *tridens* complex are similar in morphology to the minors of other species, but can be recognized by their unique propodeal structure. See Carlton (1987) for a key allowing separation of minor workers of eastern North American species.

1. North American species (Panama to southern United States, Antilles, one sp. introduced in tropical Asia, Africa) 2
– South American species (continent-wide, except the coldest and highest parts, also Galápagos) 8

2. Clypeus, in full-face view, lacking median tooth, or at most with a small blunt protuberance 3
– Clypeus, in full-face view, with a conspicuous, median tooth 7
3. Sides of head subparallel; emargination of posterior border deep, extending toward frons as a median rugose furrow; distinct propodeal carinae originating near junction of propodeal dorsum and declivity and extending forward toward anterior edge of propodeum; petiolar ventral process small, rarely flange-like; coastal plain of the Carolinas and Georgia, Florida west to Texas, Central America, Antilles (also South American, widely introduced in Old World tropics) .... *geminata*
– Sides of head distinctly divergent toward occiput; occipital furrow shallower, not rugose; propodeal carinae lacking or at most developed only at junction of basal and declivous propodeal faces (rarely a lobe- or tooth-like flange at junction of dorsal and declivous faces of propodeum); petiolar ventral process developed as ventral flange or lobe on larger specimens 4
4. Larger specimens with HW $>$ 1.5 mm; in largest workers a pair of short, longitudinal carinae, or flange- or tooth-like dorsolateral lobes near junction of basal and declivous propodeal faces .... *geminata* × *xyloni*
– Largest specimens with maximum HW $\leq$ 1.48 mm; propodeum always lacking dorsolateral carinae or flanges 5
5. Eye with 70–80 pigmented facets; head and thorax red to dark brown; gaster mostly brownish black except for large spot on first tergite of many specimens; Carolinas to southern Georgia west to California and Mexico .... *xyloni*
– Eye with 40–60 pigmented facets; yellowish red to reddish yellow, tergites may be margined with brown 6
6. In workers with HL $>$ 1.20 mm, clypeal carinae weakly developed, carinal teeth rounded and indistinct or entirely lacking in full-face view; pilosity reduced, often lacking entirely on posterior half of pronotum, mesonotum with 8–15 erect setae; cephalic pilosity mostly arising from very small punctures; anterior ventral process of petiole often nearly as large as eye in largest workers; southern Texas to Arizona, desert and semiarid Mexico .... *amblychila*
– Clypeal carinae projecting as distinct teeth from the clypeal surface even in largest workers, carinal teeth conspicuous in full-face view; pilosity abundant and evenly distributed on pronotal dorsum; mesonotum with 18–30 erect setae; cephalic pilosity arising from conspicuous foveolae; petiolar ventral process usually a longitudinal flange with the ventrally projecting anterior lobe, this notably smaller than eye; southern Texas to California, desert and semiarid Mexico .... *aurea*
7. Head and scapes brownish black, as dark as gaster or only slightly lighter; elongate triangular mark on frons barely or not at all visible; yellowish tergal spot with a definite posterior border usually present; head subelliptical to weakly ovate and relatively narrow in frontal view (Fig. 54), CI 90–96 in largest workers; pronotal dorsum medially concave; pronotum with humeral bosses; northern Mississippi, northwestern Alabama .... *richteri*
– Head, scapes and thorax reddish brown, distinctly lighter than gaster; elongate triangular mark on frons conspicuous, dark brown to black; spot on first tergite lacking, or if present, spot dusky reddish and grading indistinctly into darker posterior band; head ovate to weakly cordate and broader in frontal view (Fig. 50), CI 95–100 in largest workers; humeral bosses lacking or indistinct, anterior portion of pronotum evenly rounded when viewed dorsally; SE U.S., Puerto Rico .... *invicta*
7c. Intermediate in some of the characters in 7a and 7b; most often with the basic color pattern of a "washed out" *S. richteri,* head and thorax more brownish or mottled than gaster; gaster spot dusky with posterior margin indistinct; elongate triangular

streak on frons visible, and head ovate to weakly cordate; northeastern Mississippi, northern Alabama and northwestern Georgia .... *richteri* × *invicta*

8. Monomorphic, CI ≤ 90 in all workers, AL of largest workers rarely exceeding 1.3 mm; (if values of CI and/or AL larger, postpetiole globular and notably higher and broader than petiole) 9

– Polymorphic, large series from mature colonies always containing some workers with CI ≥ 90 (head of *S. weyrauchi* from the mountains of Peru often not so broad); AL of largest workers 1.3–2.0 mm 11

9. Eyes small, with 6–7 facets in greatest diameter; postpetiole as high or higher than petiole in profile, globular and notably broader than petiole; head, thorax, and appendages uniform straw yellow, gaster sometimes with faint brownish banding at posterior edge of tergites; Amazonian forest .... *virulens*

– Eyes larger, with 8–10 facets in greatest diameter; post petiole notably lower than petiole in profile, little or not at all broader than petiole; color various; catinga and cerrado regions of eastern and central Brazil 10

10. Propodeum, aside from dorsolateral carinae, weakly sculptured and somewhat shining; color nearly uniform brownish black; northeastern Brazil .... *tridens*

– Propodeum, in addition to dorsolateral carinae, densely sculptured and matt, especially laterally; head and thorax yellowish red to dark brown; gaster brownish black; cerrados, open woodlands and disturbed sandy soil areas of central and southern Brazil .... *substituta*

11. Head of major subquadrate or weakly trapezoidal (head may be wider in front of eyes, flaring near base of mandibles); posterior border deeply emarginate with strongly convex "temples"; with median rugose furrow extending forward to frons; emargination of posterior border extending to frons as a rugose furrow; propodeum of large and some smaller workers with distinct dorsolateral carinae and other dorsal sculpture; Venezuela to Peru, western Amazonia, Caribbean and Atlantic coastal region south to Bahia, Brazil, also Galápagos Islands (introduced?) .... *geminata*

– Head of major ovate or cordate, or even if subquadrate, with at most a weakly emarginate posterior border, and never with rugose furrow extending forward to frons; propodeum of even largest workers without longitudinal carinae dorsally, at most with bosses at meeting of dorsal and declivous faces 12

12. Scapes of any size worker notably failing to reach posterior border of head; species of western South American coastal region 13

– Scapes of small and media workers easily reaching or exceeding posterior border of head; species occurring east of the Andes from Guianas, Venezuela to Argentina, (one species from grasslands above 2,000 m elevation in the Peruvian Andes) 14

13. Eyes of major with 50–60 facets (minors have 40 or fewer); color mostly dark brown; Chile to southern Peru (introduced in Colombia?) .... *gayi*

– Eyes of major with 70–90 facets (minors have 50 or more); color usually uniform reddish; Peru .... *bruesi*

14. Larger species, AL exceeding 1.75 mm (up to over 2.0 mm) in largest workers of most series 15

– Smaller species, AL rarely in excess of 1.7 mm in even largest workers of most series (rarely up to 1.80 mm) 18

15. Color of major workers mainly brown to nearly black 16

Color of major mainly yellowish or reddish, often with only the gaster notably darker 17

16. Smaller species, HL of majors 1.45–1.55 mm, but eye of largest workers relatively (and often absolutely) larger, OI 18–20 in large majors; head mostly dark brown to brownish black; in contrast, distal portion of clypeus, head near base of mandible,

and (usually) area around dark median frontal sulcus distinctly lighter yellowish brown; Buenos Aires and La Pampa Provinces, Argentina, Uruguay, north to Santa Catarina, Brazil .... *quinquecuspis*

– Larger species, HL 1.6–1.75 mm in largest workers, but eye of largest workers relatively (and often absolutely) smaller than above species, OI 16–18 in large majors; head uniform reddish brown or gradually fading anteriad to a slightly lighter reddish brown; distal portion of clypeus, sides of head anterior to eye, and frons faintly or not at all chromatically distinct from posterior portions of head, median frontal streak absent or very faint; southeastern Brazil .... *megergates*

17. Median ocellus usually lacking; outer surface of mandible weakly shining ("sericeous") at low magnification due to close-set longitudinal costulae; thorax pilosity yellowish, the longest setae over 3× as long as the shortest, the longest setae curved; sculpture on rear face of postpetiole including transverse striae or rugulae, at least mesially, dorsal surface of postpetiole usually shiny; western Argentina, Bolivia .. .. *interrupta*

– Median ocellus often present; outer surface of mandible usually shining mesially, costulae obsolescent; thorax pilosity usually flattened basally, reddish, not curved; on largest majors, the longest setae usually little or no more than 2× the length of the shortest (less often but not uncommonly longer); sculpture on rear face of postpetiole punctate or shagreened, usually extending onto dorsal surface, lacking transverse striae or rugae, or these faint; native in Uruguay, Entre Rios Province and adjacent parts of bordering provinces in Argentina; apparently introduced at Cochabamba, Bolivia .... *macdonaghi*

18. Pronotum low and nearly flat or weakly convex in profile; gaster black, legs yellow (yellowish brown in darker specimens); head and thorax usually clear yellowish red with some black or brownish black markings in the occipital area, varying to uniformly brownish black (especially in vicinity of Cochabamba, Bolivia); western Argentina and Paraguay, north to Bolivia in Andean foothills .... *electra*

– Pronotum higher, angular or strongly convex in profile; color various but never with all black gaster and yellow legs 19

19. Area immediately behind and above metapleural spiracle finely punctate or striate-punctate; southern half of Mato Grosso, Mato Grosso do Sul, Brazil .... *pusillignis*

– Area surrounding metapleural spiracle shining and smooth 20

20. Pronotal dorsum in posterodorsal view mesially concave; anterolateral bosses giving a squared-off appearance to anterodorsal rim of pronotum; head uniformly brownish black; mandibles usually brownish yellow; frons without dark median streak or this barely distinct from remainder of frons; gaster usually with a distinct brownish yellow spot on tergite I; SE Brazil to E-central Argentina .... *richteri*

Pronotal dorsum in posterodorsal view usually flat or weakly convex; pronotum lacking anterolateral bosses; or if these present, head yellowish, at least near mandibular bases and clypeus and often more extensively 21

21. Dark median frontal streak usually lacking, but even when present, sculpture on rear face of postpetiole limited to lower ½ of its surface and usually poorly developed, typically with interstrial spaces shiny 22

– Dark median frontal streak present, but even when inconspicuous, sculpture on rear face of postpetiole of large workers covering at least lower half, often lower ¾ or more, consisting of transverse rugose striae with variably developed interstitial punctation obscuring the shininess of interstrial spaces 23

22. Larger species, AL 1.4–1.6 mm (rarely 1.7 mm) in large workers; piligerous foveolae usually very small, inconspicuous; Orinoco drainage, Guianas, Amazonia and along rivers in bordering regions, also southeastern Brazil (Cephalic pilosity of queen about

0.3–0.33 mm long; queens with gaster pilosity arising from small, inconspicuous foveolae) .... *saevissima*

– Smaller (and much rarer) species; AL < 1.4 mm in even the largest workers; piligerous foveolae on head and pronotum of some workers conspicuous, 5–10× as wide as base of seta; Mato Grosso do Sul to southeastern Brazil and Misiones, Argentina

– (Cephalic pilosity of queen about 0.15–0.2 mm long; gaster pilosity arising from conspicuous foveolae nearly or indeed as large as those of head and thorax) ... *pythia*

23. Head narrow, CI of even the largest known workers around 90; Peruvian Andes, 2,000–3,500 m elevation .... *weyrauchi*

– Head broader, CI 95–100 in large workers; lowland species, western Amazonia, south through Mato Grosso, eastern Bolivia, Paraguay and southeastern Brazil to Santa Fé Province, Argentina .... *invicta*

Species descriptions

The species descriptions include synonymy, measurements and indices, worker diagnosis, notes (discussion) and distribution. The notes section presents taxonomic and natural history information. Distribution is summarized by representative collection localities delimiting the known extremes of the geographic range of each species.

VIRULENS COMPLEX

A single Amazonian and Brazilian coastal forest species constitutes this complex, which is probably not a true member of the *S. geminata* group. It is characterized by monomorphic, yellowish workers with small eyes, long scapes, and inflated postpetiole. This species is compared to the minor workers of the polymorphic species in the following diagnosis.

Solenopsis virulens, **New Status**
Figs. 25–27

Myrmica virulens Fred. Smith, 1858:132. Syntype workers. BRAZIL. Amazonas. Ega (=Tefe). Bates. (BMNH, examined.)

Solenopsis bondari Santschi, 1925:236. Syntype workers. BRAZIL. Bahia. 891 (=1891?). Bondar. (NMB, examined.) NEW SYNONYMY.

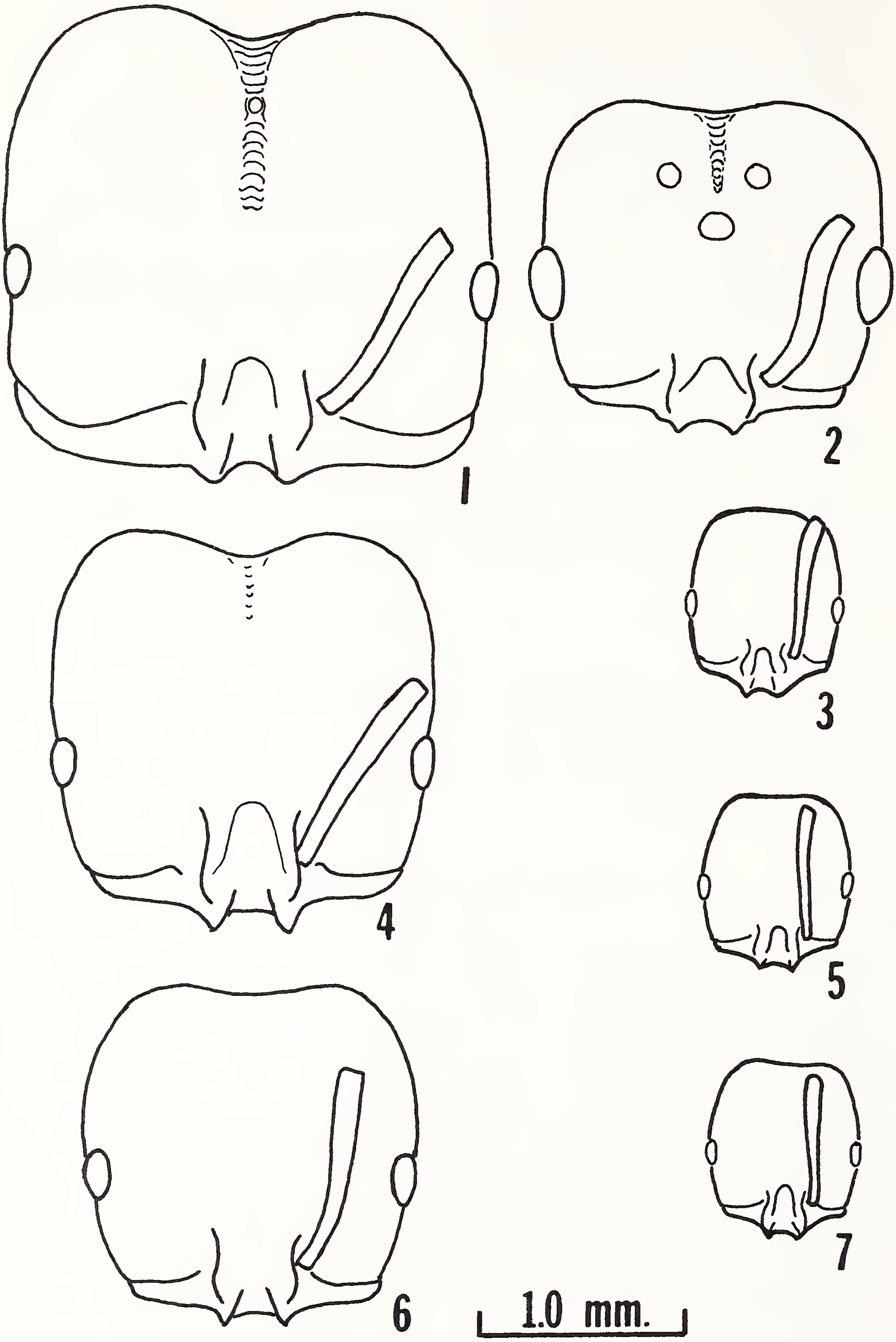
S. bondari: Kempf and Brown, 1968:99.

S. virulens: Kempf and Brown, 1968:99. (Apparently first used in this combination by these authors, it was treated as *nomen oblitum* by them. Dr. Brown now agrees that the older name should stand.)

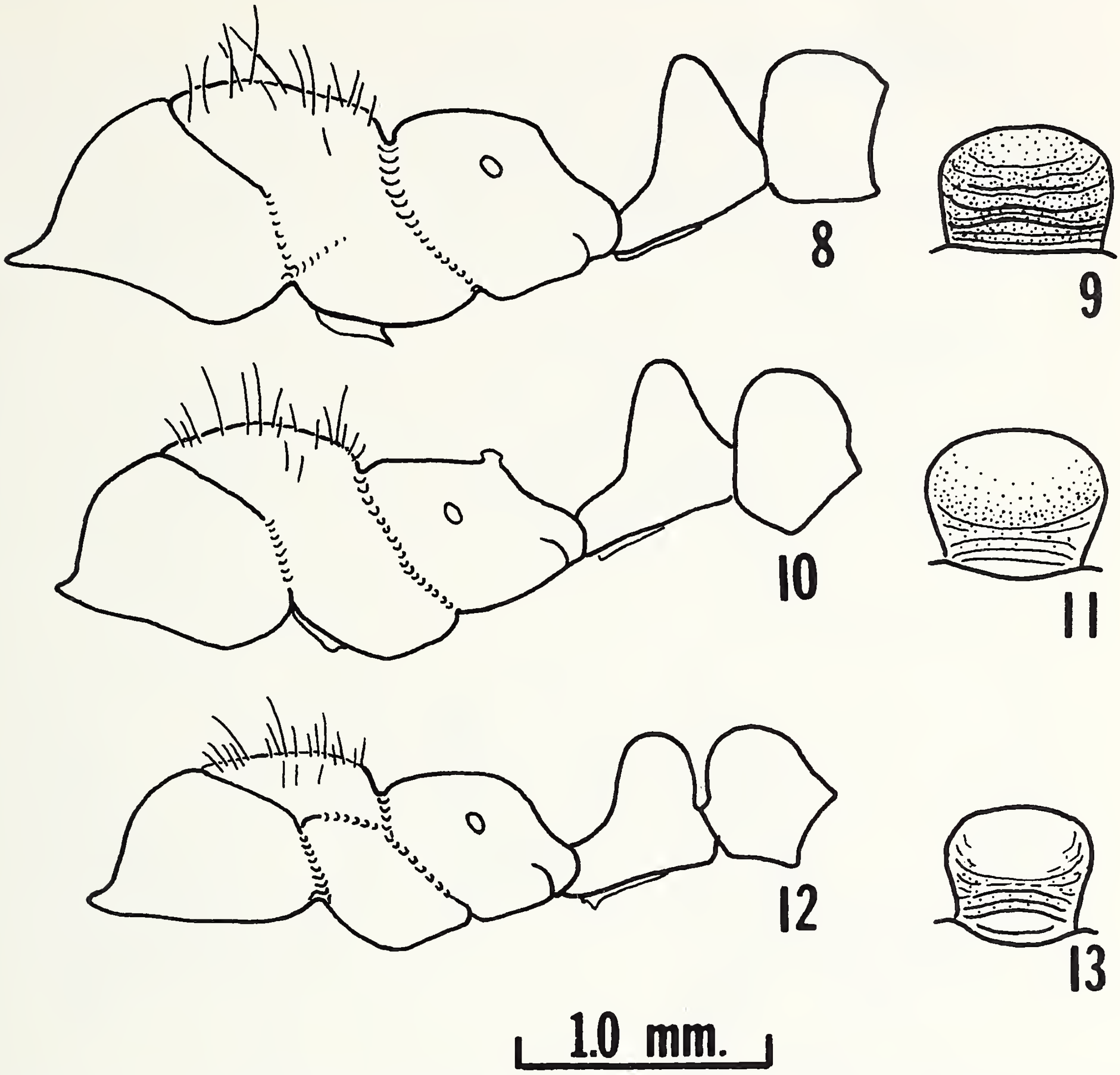
S. (*Solenopsis*) *bondari*: Creighton, 1930:46. Description of workers Creighton considered "cotypes" from Kartabo, British Guiana. (NMB?, not examined.)

MEASUREMENTS AND INDICES: HL 0.78–1.00, HW 0.68–0.93, SL 0.68–0.88, EL 0.11–0.14 (0.15), PW 0.45–0.60, AL 0.98–1.34, CI 86–95 (97), SI 91–104, OI 13–15 (16). N = 25.

WORKER DIAGNOSIS. Monomorphic. Head (ffv) elliptical, with sides more convex than in minors of other species; posterior border weakly concave, concavity



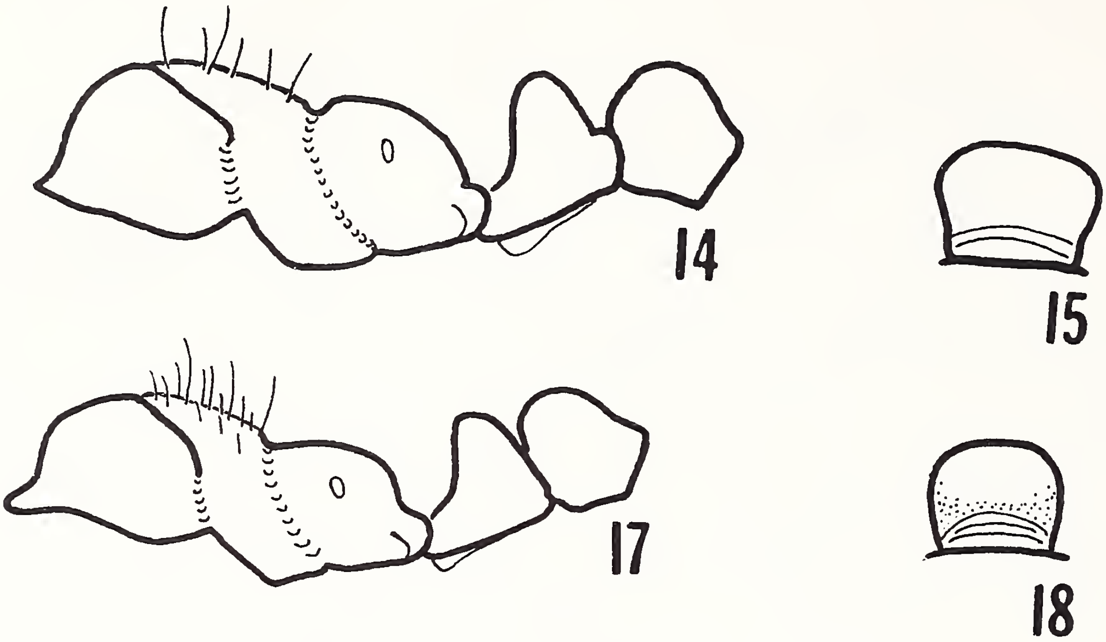
Figs. 1–6. North American *Solenopsis* heads, full face view. 1–3. *S. geminata*; major, queen and minor. 4–5. *S. geminata* × *xyloni*; major and minor. 6–7. *S. xyloni*; major and minor.

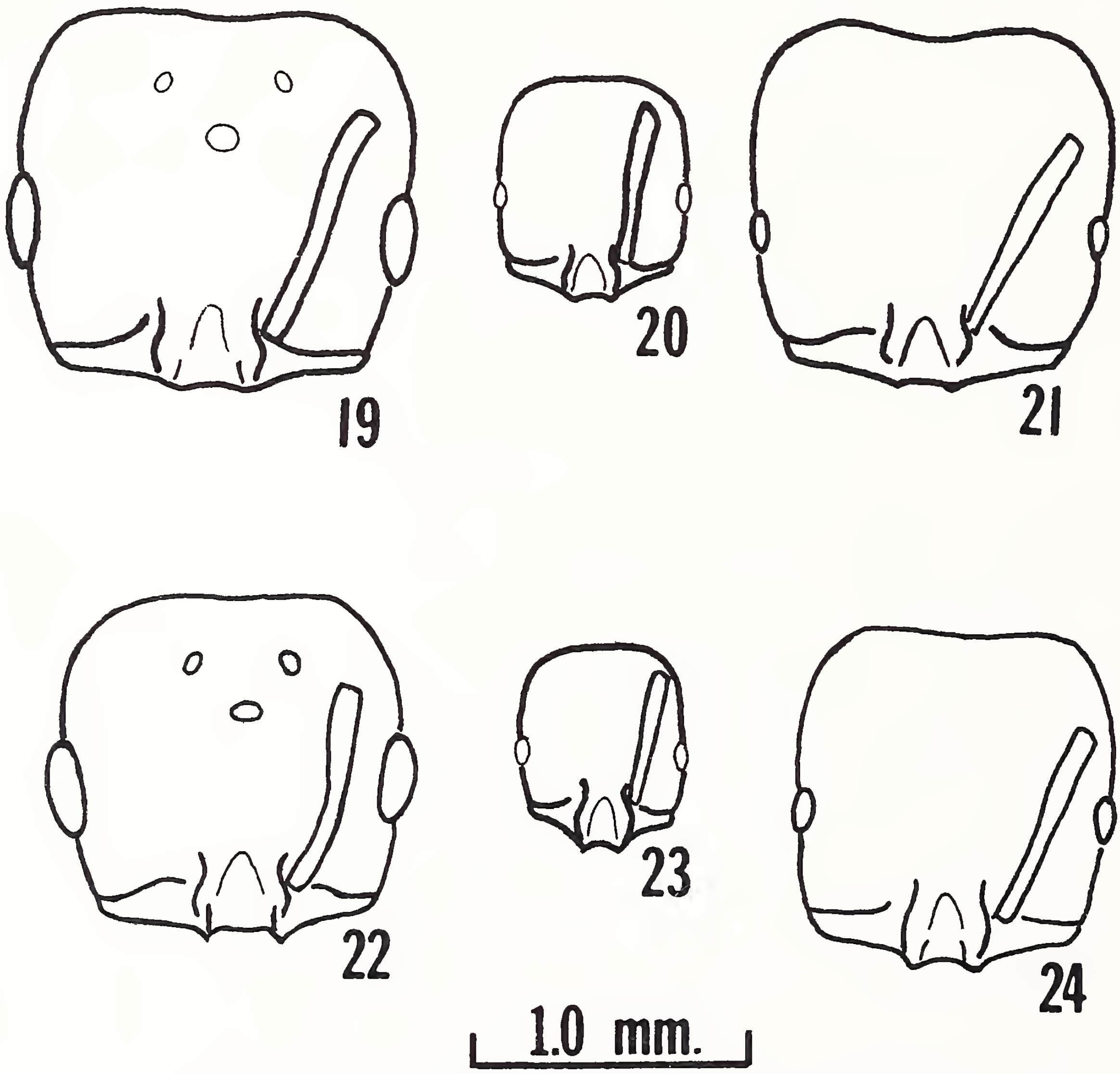


Figs. 8–13. North American *Solenopsis* trunk profiles and postpetiole rear views of major workers. 8–9. *S. geminata.* 10–11. *S. geminata* × *xyloni.* 6–7. *S. xyloni.*

about as wide as distance between frontal lobes (usually) or less; median clypeal tooth poorly developed, or lacking altogether; clypeal carinae weakly produced distally as a pair of (usually) blunt, short teeth; mandibles narrow and weakly curved, less curved than in minors of other species; mandibular costulae well-developed; eye (lv) small, greatest diameter with 5–6 facets, least diameter with 4; scapes (ffv) long, even compared to minor workers of most polymorphic species, scape length exceeding distance between base of scape and occipital corners by 1.3–2.0 × apical diameter of scape; anterior pronotal border (pdv) convex, anterolateral angles distinct but lacking humeral bosses; promesonotal suture obsolete or at most indicated by a shallow, acute-angular impression (not visible in lv); petiolar peduncle longer than base of node, straight to weakly concave ventrally; profile of petiolar node with moderately sharp crest; outline of petiolar node (pdv) globular with shallow median concavity; profile of postpetiolar node in profile globular, as high as that of petiole; postpetiole (pdv) 1.25–1.33 × as wide as petiole.

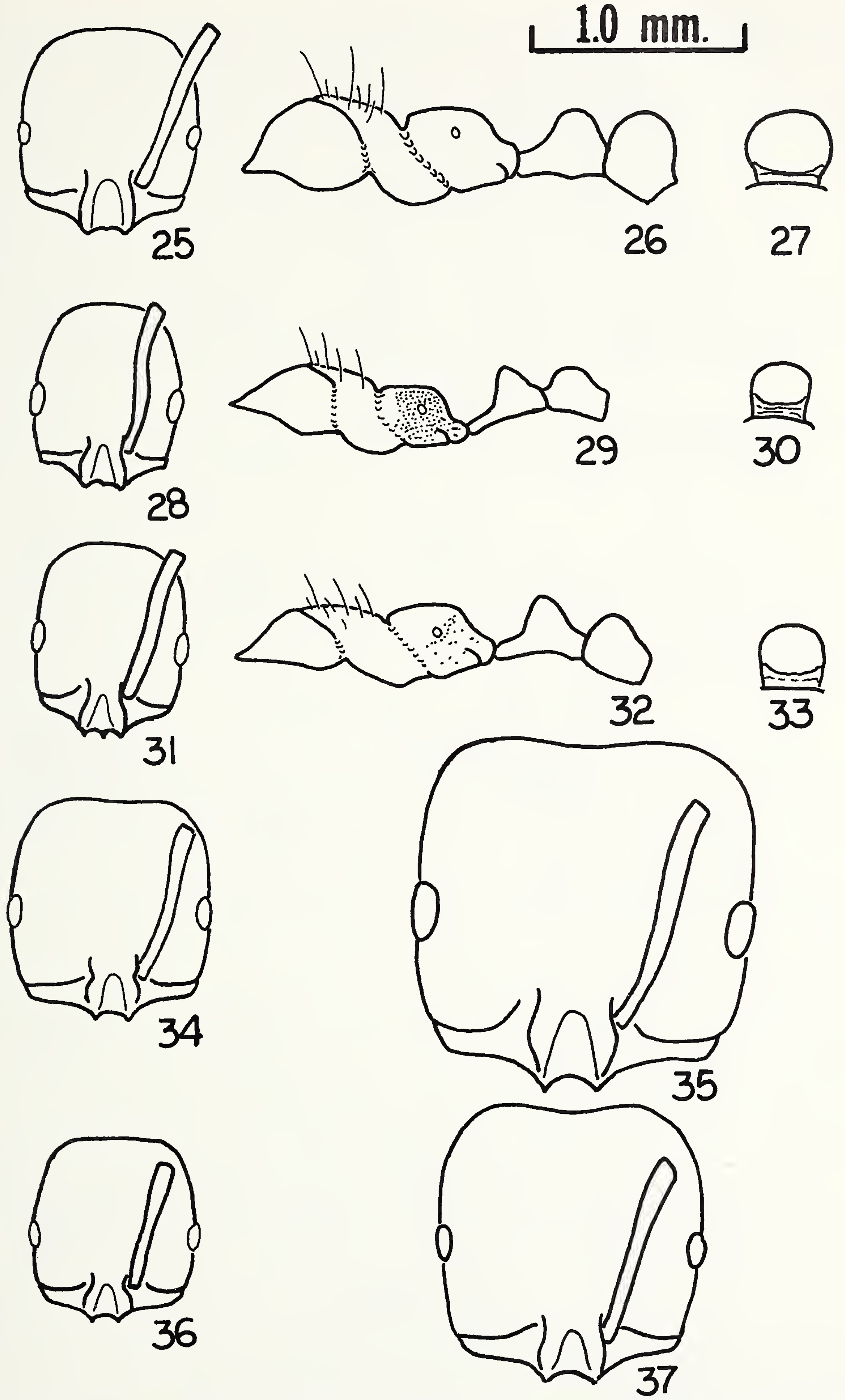
Piligerous foveolae of head and thoracic dorsum conspicuous, 0.006–0.013 mm





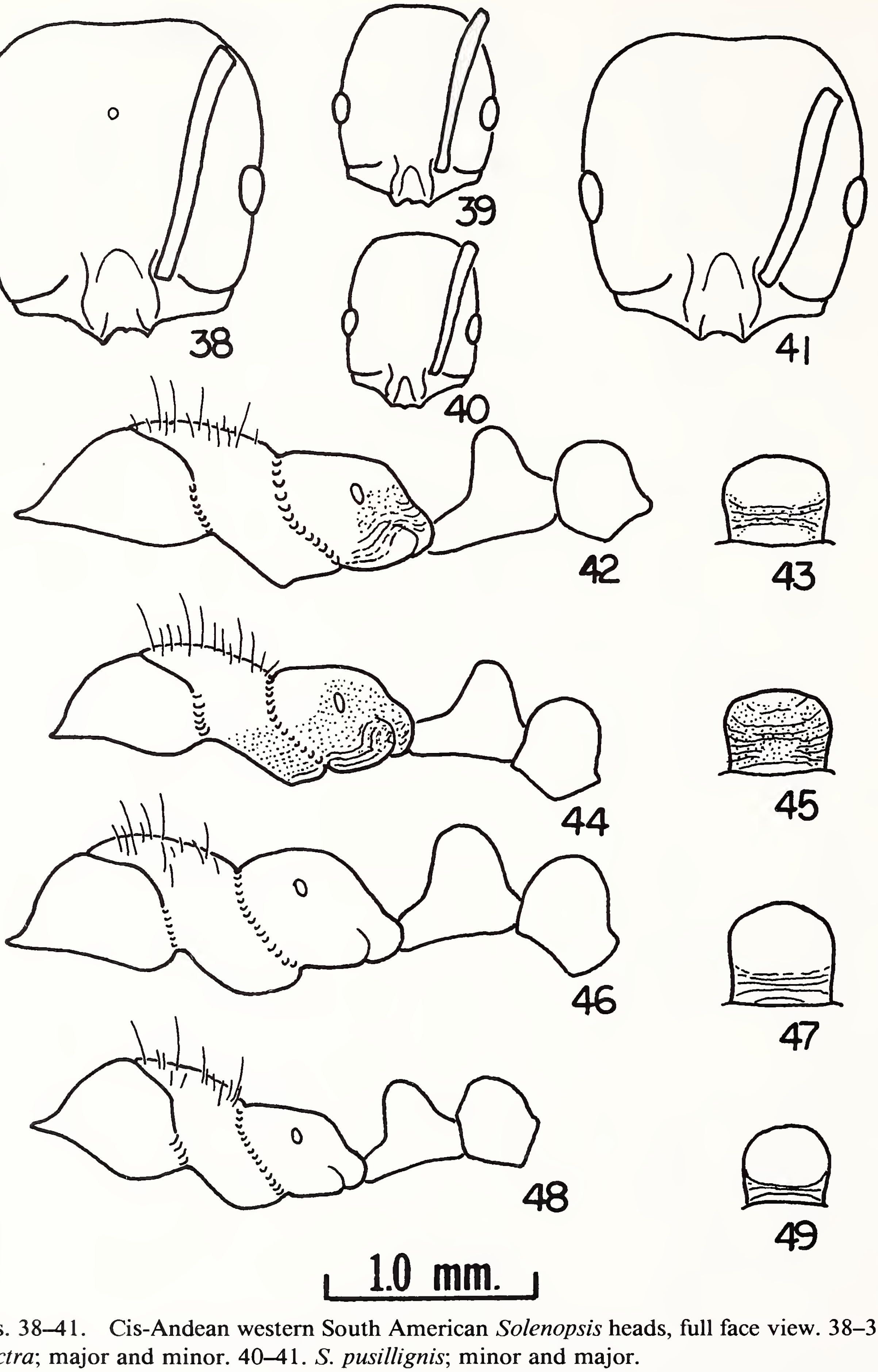
Figs. 14–18. North American desert *Solenopsis* trunk profiles and postpetiole rear views of major workers. 14–15. *S. amblychila*. (16 deleted.) 17–18. *S. aurea*.

Figs. 19–24. North American desert *Solenopsis* heads, full face view. 19–21. *S. amblychila*; queen, minor and major. 22–24. *S. aurea*; queen, minor and major.



Figs. 25–33. Monomorphic *S. geminata* group species; heads, full face view, trunk profiles, and postpetiole rear views. 25–27. *S. virulens.* 28–30. *S. substituta.* 31–33. *S. tridens.*

Figs. 34–37. Trans-Andean western South American *Solenopsis* heads, full face view. 34–35. *S. bruesi,* 36–37. *S. gayi,* minor and major.



Figs. 38–41. Cis-Andean western South American *Solenopsis* heads, full face view. 38–39. *S. electra*; major and minor. 40–41. *S. pusillignis*; minor and major.

Figs. 42–49. Western South American *Solenopsis* trunk profiles and postpetiole rear views of major workers. 42–43. *S. electra*. 44–45. *S. pusillignis*. 46–47. *S. bruesi*. 48–49. *S. gayi*.

in diameter; sculpture of mesometapleuron (lv) consisting of longitudinal rugae with interstitial punctation dulling the interrugal spaces; dorsum of propodeum unsculptured; area surrounding propodeal spiracle unsculptured; ventral process consisting of 1–3 small tooth-like projections; dorsum of petiolar node unsculptured; posterior face of petiolar node unsculptured or with faint areolation on the lower portion; node of postpetiole unsculptured.

Pilosity of head and promesonotum, 0.1–0.36 mm in length.

Color pale yellow; sometimes with posterior portions of gastral tergites slightly brownish.

NOTES. This species may have an origin independent of the *S. geminata* group from *S. globularia*-like ancestors. Its sting is reputed to cause a reaction much more painful than that of typical fire ants. Although common and much collected, sexuals of this species are not known.

DISTRIBUTION. *S. virulens* inhabits all of northern South America in forested areas from the base of the Andes to the Atlantic coast, south to Bolivia and Bahia, Brazil.

TRIDENS COMPLEX

This is a small complex of 2 species from the cerrado and catinga vegetation of central and northeastern South America. Both species have monomorphic workers with long scapes, well developed propodeal carinae and an elongate petiolar peduncle.

Solenopsis substituta, **New Status**
Figs. 28–30

Solenopsis tridens var. *substituta* Santschi, 1925:236. 1 worker, 2 queen syntypes. BRAZIL. São Paulo. Pitangueiras. Luederwaldt. (NHM, examined.)
S. (*Solenopsis*) *tridens* var. *substituta*: Creighton, 1930:95. Worker, queen.

MEASUREMENTS AND INDICES: HL 0.71–0.82, HW 0.59–0.69, SL 0.63–0.70, EL 0.13–0.15, PW 0.39–0.51, AL 0.94–1.12, CI 80–86, SI 100–107, OI 17–20. N = 20.

WORKER DIAGNOSIS. Monomorphic. Head (ffv) obovate (broader anteriorly), with sides straight to weakly convex anterior to eye; convex and converging posteriad behind eye; posterior border convex, median concavity lacking; median clypeal tooth well-developed, truncate or acuminate, protruding nearly or indeed as far as carinal teeth; clypeal carinae prominent, sharp-crested, produced distally as a pair of sharp teeth; mandibular costulae weakly developed, 4–5 in number when visible; eye (lv) relatively large, greatest diameter with 9–10 facets, least diameter with 6–7; scapes (ffv) long, SL exceeding distance between base of scape and occipital corner by 0.8–1.5× apical diameter of scape; anterior pronotal border (pdv) with anterolateral corners distinct, bearing small, smooth bosses; promesonotum (lv) without anterior declivity mesially, dorsum a continuous convexity from base of cervical collar to mesothoracic declivity; propodeal dorsum convex, sloping, descending through right, or weakly obtuse angles to declivous face; petiolar peduncle longer than base of node, ventrally concave; profile of petiolar node cuneate with dorsum truncate; postpetiole 1.1–1.2× as wide as petiole.

Integument mostly smooth; piligerous foveolae of head and thoracic dorsum mostly

minute, not readily visible, but a few on vertex up to 0.008 mm in diameter; dorsum of propodeum with lateral carinae, with faint areolation between them; area surrounding propodeal spiracle matt, sculptured as adjacent metapleuron; declivous face of propodeum with transverse striae and areolation contiguous with those of metapleuron, but of larger "mesh"; petiolar peduncle dorsally areolate; venter of petiole concave, with ventral process consisting of concavity between 2 blunt protuberances; petiolar node and entire postpetiole unsculptured.

Pilosity of head and promesonotum 0.08–0.25 mm in length.

Bicolored; head, thorax, waist and appendages brownish-red, gaster dark brown to black.

NOTES. *S. substituta* is found nesting in sandy, or less often, gravelly soils in cerrado vegetation. It seems to prefer sites where there has been grazing or foot traffic.

It is not certain that this taxon will continue to be recognized as a distinct species when further samples are studied coming from the area between that from which it is now known and that from which its sister species *S. tridens* is known. I have separated the 2 taxa in the light of their apparently disjunct ranges and distinct sculpture and color.

DISTRIBUTION. The types (examined) were collected at Pitangueira, São Paulo, Brazil. Other specimens studied come from Brazil, namely vicinity of Cuiabá, Mato Grosso and various locations in São Paulo State.

Solenopsis tridens
Figs. 31–33

Solenopsis tridens Forel, 1911:298. 5 syntype workers. BRAZIL. Bahia. Villa Nova (=Vila Nova). Garve (MHNG, examined).

S. (*Solenopsis*) *tridens*: Creighton, 1930:94. (No specimens examined; translation of Forel's original description.)

MEASUREMENTS AND INDICES: HL 0.73–0.80, HW 0.61–0.66, SL 0.65–0.69, EL 0.13–0.14, PW 0.42–0.45, AL 1.04–1.06, CI 81–85, SI 103–107, OI 18 (all). N = 4.

WORKER DIAGNOSIS. Monomorphic. Closely resembling *S. substituta,* but differing as follows: mandibular costulae better developed, especially basally, usually 5 in number, obsolescent in distal ⅓ to ½ in some specimens; dorsum of propodeum with ridge-like bosses at juncture of dorsal and declivous propodeal faces, but area between bosses smooth, shining; area surrounding propodeal spiracle unsculptured below, unsculptured to weakly striate above spiracle; declivous face of propodeum unsculptured; venter of petiolar peduncle with longitudinal median carina weakly developed and this only anteriorly, ventral process obsolete.

Color uniform blackish brown, with somewhat lighter appendages.

NOTES. The biology of *S. tridens* is unknown. This species may be the northern part of clinal variation that includes what I have called *S. substituta,* but I have seen no intermediate specimens. DISTRIBUTION. The types (examined) were collected at Villa Nova (now spelled Vila Nova), Bahia, Brazil.

GEMINATA COMPLEX

This complex contains 3 subcomplexes collectively distinguished by their peripheral (northern and western) distribution, strongly-developed polymorphism, rela-

tively short scapes, often well developed inferior petiolar process, and by the reduction or loss of at least the median clypeal tooth.

The *geminata* subcomplex apparently contains one highly variable species ranging from northern South America to southeastern United States. This species has a characteristic hypertrophied major worker head, with thick, strongly curved mandibles whose teeth are often worn off by milling seeds.

The *xyloni* subcomplex comprises 3 species from Mexico and the southern United States. Major workers usually have a conspicuous, transparent flange on the ventral process of the petiolar peduncle. The demonstration of hybridization between *S. geminata* and *S. xyloni* (Hung and Vinson, 1977) has been corroborated morphologically in this study and is evidence for the close relationship of the *xyloni* and *geminata* subcomplexes, their disparate morphological features notwithstanding.

Finally, *S. bruesi* of western South America is reminiscent of the *xyloni* subcomplex of North America in its relative tolerance for drier and cooler climates, and in the reduction or absence of the median clypeal tooth. *S. gayi* sometimes has a well developed petiolar ventral process as in some North American species. Here, the 2 species are called the *gayi* subcomplex.

GEMINATA SUBCOMPLEX

Solenopsis geminata

Figs. 1–3, 8, 9

NOTE: All synonymies listed below which are not attributed to any other author are based on the treatment of this species by Creighton (1930). These synonymies are accepted based on the overall strength of Dr. Creighton's study, even though the specimens were not examined in this study.

Atta geminata Fabricius, 1804:423. Queen. South America. (Not examined.)
Solenopsis mandibularis Westwood, 1841:87. Worker. (Not examined.)
Atta rufa Jerdon 1852:106. Worker. India. (Not examined.) (Synonymy by Ettershank (1966:136).)
Solenopsis cephalotes F. Smith, 1858:149. Worker. (Not examined.)
Atta clypeata F. Smith, 1858:169. Queen, male. (Not examined.)
Crematogaster laboriosus F. Smith, 1860:109. Worker. (Not examined.)
Diplorhoptrum drewseni Mayr, 1861:71. Worker. (Not examined.)
Myrmica glaber F. Smith, 1862:34. Worker. Guiana. (BMNH, examined.)
Myrmica polita F. Smith, 1862:34. Worker (minims). Guiana. (BMNH, examined.)
Solenopsis saevissima: Mayr, 1862:751. MISIDENTIFICATION.
?*Atta Lincecumii* Buckley, 1867:344. Worker. USA. Texas. (Not examined.)
?*A. coloradensis* Buckley, 1867:346. Worker. USA. Texas. (Not examined.)
Solenopsis geminata: Mayr, 1867:109; Forel, 1881:10; Wheeler, 1908:424; Forel, 1909:268; Ettershank, 1966:136, Figs. 95–99.
S. geminata var. *rufa*: Wheeler, 1907:272. Forel, 1909:268. Bingham, 1903:158.
S. geminata var. *diabola* Wheeler, 1908:424. Worker. Syntype workers. USA. Texas. Austin. Wheeler. (MCZ, examined.)
S. geminata var. *nigra* Forel, 1908:45. Syntype workers. Costa Rica. Biolley. (MNHG, examined.); Forel, 1909:268; Forel, 1913:23. (Synonymy by Ettershank, 1966:136.)
S. eduardi Forel, 1912:12. Worker. COLOMBIA. Magdalena. Rio Frio. (MHNG, examined.) (Synonymy by Ettershank, 1966:136.)

S. geminata var. *innota* Santschi, 1915:257. Worker, queen and male syntypes. GABON. 1909 (workers) and 1914 (alates). F. Faure. (NMB, examined.) (Synonymy by Ettershank, 1966:136.)
S. geminata medusa Mann, 1916:447. Syntype workers. BRAZIL. Rio Grande do Norte. Ceará-Mirim. Mann. (MCZ, examined.) (Synonymy by Ettershank, 1966: 136.)
S. geminata galapageia Wheeler, 1919:272. Worker, queen syntypes. ECUADOR. Galapagos Islands. Santa Cruz Isl. (Charles or Indefatigable.) (MCZ, LACM, examined.) (Synonymy by Ettershank, 1966:136.)
S. eduardi: Santschi, 1924:13. (Not examined.) (Synonymy by Ettershank, 1966:136.)
S. eduardi var. *perversa* Santschi, 1924:13. Syntype workers. BRAZIL. Pernambuco. Tapeza. Guenther. (NHMB, examined.) (Synonymy by Ettershank, 1966:136.)
S. eduardi var. *bahiaensis* Santschi, 1925:236. Syntype workers. BRAZIL. Bahia. 892 (=1892). Bondar. (NMB, examined.) (Synonymy by Ettershank, 1966:136.)
S. (*Solenopsis*) *geminata*: Creighton, 1930:59. Worker, queen, male.
S. (*Solenopsis*) *geminata galapageia*: Creighton, 1930:65. Worker, queen.
S. (*Solenopsis*) *geminata rufa*: Creighton, 1930:66. Worker, queen, male.
S. (*Solenopsis*) *geminata eduardi*: Creighton, 1930:67. Worker.
S. (*Solenopsis*) *geminata medusa*: Creighton, 1930:68. Worker, queen.

MEASUREMENTS AND INDICES: HL 1.06–2.20, HW 0.98–2.33, SL 0.78–1.14, EL 0.15–0.29, PW 0.57–1.06, AL 1.18–2.08, CI 92–108, SI 47–84, OI 11–16. N = 34.

WORKER DIAGNOSIS. Head (ffv) subquadrate to subtrapezoidal (sides often divergent or flaring anteriorly, especially in specimens from southern Central America and eastern South America), with sides straight to weakly convex and parallel to weakly divergent anteriad (sides weakly convergent anteriad in specimens from souther Texas), often slightly indented just anterior to eyes; posterior border with deep angular median emargination between two nearly hemispherical lobes ("temples"); emargination 1.0–1.5× as wide as distance between apices of frontal lobes; median clypeal tooth lacking or (rarely) rudimentary; carinal teeth thick at base, strongly protruding, clypeal border between them concave; mandibles thick and strongly curved mesad, especially in largest individuals; mandibular teeth present in all individuals upon eclosion, but often worn off through seed-milling by larger individuals, such that apices dulled or flattened; mandibular costulae complete in smaller majors, to irregular and largely obsolete in larger majors; eye (lv) appearing small relative to hypertrophied head, greatest diameter with 9–11 facets, least diameter with 7–9; largest majors rarely with median ocellus more or less well developed; scapes (ffv) short, curved, scape failing to reach apices of occipital lobes by 0.3–0.5× SL; pronotum with rounded, at most faintly angular anterolateral corners; promesonotal suture conspicuous, approximately right-angular to weakly obtuse-angular, raised as a small boss at most anterior point; promesonotal profile (lv) formed of 2 convexities meeting at anterior mesonotal boss, pronotal profile more strongly convex and at most feebly angular; anteroventral border of mesopleuron thickened, often bearing one or more spine-like, triangular, lobate or rectangular projecting flanges; metanotal impression marked, set off by a ridge at its juncture with propodeum; propodeal

profile more or less diamond-shaped, with dorsum flat to weakly concave; descending though obtuse, carinate angles to weakly convex declivous face; petiolar peduncle as long as or a little longer than base of node; profile of petiolar node cuneate with a relatively sharp crest; postpetiole 1.02–1.08× as wide as petiole.

Piligerous foveolae of head and thoracic dorsum conspicuous and abundant, 0.025 or more in diameter, those near mouthparts and on sides of head sometimes elongate; on larger specimens, mesopleuron largely unsculptured to feebly rugose, but coarsely rugose along pleural suture and near edges of sclerite, especially anteroventrally (in smaller specimens, mesopleuron striate-punctate to coarsely rugose); dorsum of propodeum with a pair of irregular dorsolateral carinae, these best developed at juncture of dorsal and declivous faces; posteriorly, transverse striae or rugae may occur on dorsal, concave surface between carinae; area surrounding propodeal spiracle encircled by coarse, irregular rugosity; declivous face of propodeum with transverse rugae contiguous with those of metapleuron on lower portion, but on upper part more neatly aligned than, and not always contiguous with those on side of propodeum; lateral carinae usually obsolescent on all but uppermost portion of propodeal declivous face; petiolar peduncle transversely striate; base of node areolate-punctate; petiolar ventral process consisting of 1 or 2 small teeth, or rarely, a very narrow, transparent flange; dorsum and anterior face of petiolar node sparsely punctate-foveolate, sometimes dorsum with transverse striation like that on posterior face, dorsal margin weakly scalloped; posterior face of petiolar node transversely striate to weakly rugose-areolate below, sparsely sculptured, or less often sculptured as below near top, though less coarsely; sides of postpetiole rugose-punctate; venter of postpetiole dull, coarsely punctate; dorsum of postpetiole weakly scalloped, usually shiny and unsculptured or with a weaker version of sculpture below; posterior face of postpetiole transversely rugose-punctate.

Pilosity of head and promesonotum abundant, 0.13–0.37 mm in length; some pilosity often present on meso- and metapleuron.

Color highly variable, though generally fairly consistent within a colony; ranging from concolorous orange-red with only posterior portion of gaster dark brown (var. *rufa*), to nearly concolorous brownish black with only head near base of mandibles and appendages (especially distally) reddish-brown (var. *nigra*). Smaller workers tend to be darker and more uniformly colored than bigger ones. Darker *S. geminata* are possibly limited to or at least prefer more humid microhabitats, and ecological conditions during rearing may be at least partly responsible for adult coloration, but this needs study. Redder variants often are, or at least appear less sculptured than darker forms, but are more likely to have mesopleural flanges. However, I have studied samples from single colonies with virtually the entire range of color and sculpture described above, and *S. geminata* individuals may have any possible combination of color and sculpture.

NOTES. The distinctive morphology of the major of *S. geminata* is associated with its granivorous habits. It is not unusual to find caches of small seeds, in the nests of this species. In Florida at least, the seeds are usually those of panicoid grasses. The teeth of the majors, which do most of the seed milling, are usually worn off shortly after eclosion, yielding the flat-ended mandibles typical of this species. Unlike the majors of other species, those of *S. geminata* are rather slow-moving and unaggressive.

S. geminata has been introduced into both tropical Asia and Africa. The first of these populations is now distributed from Taiwan and India in the north, throughout the Malay archipelago and Polynesia in the south, but the population is highly uniform throughout this vast range, with the light reddish coloration, relatively weak sculpture, and well-developed mesopleural process typical of the form *rufa,* and may result from the successful spread of a single original introduction. The African population is less well known, but is found in tropical west Africa. It resembles the black form found in Georgia, Florida and the Antilles. The being said, it is important to point out that these color and sculpture variants do not hold up as distinct entities in their native America, where there is great variability both within and among localities.

The only population which might, in my opinion, be a distinct species among the material called *S. geminata* here is the western South American population of Colombia and Peru. This form averages smaller in all castes than *S. geminata* from elsewhere, and its sting is reputed to be more painful and to cause a pustule as do stings of the *S. saevissima* complex. The western population is apparently the source of the rather small *S. geminata* typical of the Galápagos Islands. I have been unable to find any morphological differences other than size between this form and the remainder of what I call *S. geminata,* but further study is necessary to resolve the issue.

S. geminata × *xyloni* hybrids (Figs. 4, 5, 10, 11) were confirmed by Hung and Vinson (1977) in an early use of allozymes to tackle a problem in ant systematics. They made the interesting observation that while workers were intermediate between the parent species in allozyme electrophoretic banding patterns, winged queens from the same colony showed only the *S. xyloni* pattern. I have examined a few series of this hybrid from Texas, and can confirm that winged queens from such series usually resemble *S. xyloni* morphologically, as well, though one appeared intermediate. It is possible that the generally weaker sculpture and somewhat anteriorly convergent major worker head of Texas *S. geminata* result from introgression of characteristics from *S. xyloni.*

DISTRIBUTION. *S. geminata* is apparently native from the southeast coastal plain and Florida to Texas (lacking in Alabama, Mississippi and Louisiana?) south through Central America to northern South America, including the coastal areas of northeastern Brazil, west through the Guianas to the Orinoco Basin, the western Amazon Basin and coastal areas of Peru. Populations of the Antilles and Galápagos (and possibly the southeastern U.S.A.) are probably introduced, but have been in these areas for several centuries.

XYLONI SUBCOMPLEX

Solenopsis xyloni

Figs. 6, 7, 12, 13

Solenopsis xyloni MacCook 1879:188. Worker, queen. (No types designated. Specimens studied by MacCook from Alabama, now at USNM, examined.)

S. pylades Forel 1904:172. Queen. Mexico. NEW SYNONYMY. (Examined by W. F. Buren.) (All later references to this taxon, including those by Forel, concern members of the *saevissima* complex, and not Forel's Mexican species.)

S. geminata xyloni: Wheeler 1915:395.
S. geminata maniosa: Wheeler 1915:396. Syntype workers. USA. California, Santa Barbara. (Synonymy by Creighton, 1950:232–233.) (To my knowledge, no specimens from Santa Barbara, dead or alive, have been seen since! Specimens labeled cotypes by Wheeler from various California localities were examined.)
S. (*Solenopsis*) *xyloni*: Creighton 1930:99. Worker, queen, male. Smith 1947:568.
S. (*Solenopsis*) *xyloni* var. *maniosa*: Creighton 1930:102. *Solenopsis maniosa*: Snelling 1963:9. (Invalid resurrection of taxon.)
?*Myrmica* (*Atta*) *sabeana* Buckley 1866:343. Worker. (No types.)
?*Atta brazoensis* Buckley 1866:345. Worker. (No types.)

MEASUREMENTS AND INDICES: HL 1.00–1.50 (1.57), HW 0.89–1.53 (1.58), SL 0.73–0.95, EL 0.16–0.25 (0.29), PW 0.51–0.84 (0.88), AL 1.10–1.75 (1.80), CI 89–102, SI 59–82, OI 14–19 (20). N = 38.

WORKER DIAGNOSIS. Head (ffv) weakly to distinctly cordate, with sides convex; posterior border with a concave median impression, the concavity about 1.5× or more as wide as distance between apices of frontal lobes; median clypeal tooth lacking; median clypeal seta sometimes lacking or displaced off center; clypeal carinae conspicuous, projecting apically as short, rounded teeth, the clypeal border between them straight to concave, or wavy in outline; mandibles with the usual curvature; mandibular costulae 6–7 in number, complete of obsolete mesially near inner border; eye (lv) ovate, greatest diameter with 9–11 facets, least diameter with 7–9, southwestern specimens (Mexico, Arizona, California) often have the outer ring of facets depigmented, making the eye appear smaller; scapes (ffv) short, distance between tip of scape and occipital corner about 0.25–0.45× scape length in major workers, even in smallest workers scape apex fails to reach posterior border by almost 2× apical width of scape (scape reaching or exceeding posterior border in minors of all other species except *S. amblychila* and *S. aurea*); anterolateral pronotal corners (pdv) rounded, lacking protruding angles; distal border of mesopleuron thickened, flange-like, turned outward; metanotal impression conspicuous; propodeal profile with anterior declivity usually concave, often set off from propodeal dorsum by sharp anterior border, dorsum weakly convex, descending through rounded angles to declivous face; petiolar peduncle a little shorter to slightly longer than base of node; postpetiolar node in profile lower than petiole, globular, sometimes with dorsoposterior face a little more convex than anterior face, outline of postpetiolar node (pdv) globular, or especially in larger workers with dorsal face convex, and lateral faces straight, convergent ventrad; postpetiole 1.05–1.2× as wide as petiole.

Piligerous foveolae of head and thoracic dorsum 0.01–0.02 mm in diameter; sculpture of mesometapleuron (lv) consisting of fine longitudinal rugae or striae with interstitial punctation or areolation, sculpture lacking on episternal (anteroventral) portion of mesopleuron; surface of mesopleural marginal flange roughened; dorsum of propodeum unsculptured; area surrounding propodeal spiracle usually unsculptured, or with some faint semicircular rugae behind and/or above spiracle; declivous face of propodeum with transverse striae contiguous with those of metapleuron; petiolar peduncle and base of node weakly areolate; venter of petiole with longitudinal median carina and ventral process consisting of a more or less triangular, transparent, jagged edged flange, this always significantly smaller than eye, sometimes narrow

flange continues backward along median carina; petiolar node largely unsculptured except piligerous foveolae; dorsum of postpetiole unsculptured other than piligerous foveolae, or rarely weakly transversely striate-punctate; posterior face of postpetiole mostly shiny above, shiny to transversely rugose below.

Pilosity of head and promesonotum abundant, 0.08–0.35 mm in length; some pilosity often present on meso- and metapleuron.

Color highly variable, though generally fairly consistent within a colony; ranging from concolorous orange-red (var. *maniosa*) with only posterior portion of gaster dark brown, to nearly concolorous brownish black with only head near base of mandibles, and appendages (especially distally) brownish-red. Smaller workers, unlike those of *S. geminata,* tend to be colored like larger workers of the same colony. The darkest color variants occur interspersed among redder ones from Texas to Arizona, south into Mexico. The former are possibly limited to or at least prefer more humid microhabitats (Dr. M. J. Plagens, Phoenix, Arizona, pers. comm.) as in *S. geminata*; the reddest ones occur in the deserts of California.

NOTES. The pale California desert samples of *S. xyloni* are barely distinguishable from *S. aurea,* and single individuals will probably be impossible to determine with certainty. The form *maniosa* (which includes these desert samples) is no more than a slightly smaller variant of *S. xyloni,* at least morphologically. Future studies of the biochemistry or genetics of *S. xyloni* may reveal some cryptic speciation in this taxon, but I have been unable to find any morphological justification for separating the form *maniosa.* The variation in *S. xyloni* is no greater than the sort seen in other widely distributed, abundant species of fire ants.

See notes on *S. geminata* for discussion of hybridization with *S. geminata.*

No type locality (nor any type specimens) were designated in the original description of this species. I have designated a worker from Baton Rouge, Louisiana as holotype, and the remainder of the accompanying series with the same collection data as paratypes. The specimens are housed in the USNM.

DISTRIBUTION. *S. xyloni* is found across the southern United States from the Carolinas and Georgia, through lowland Tennessee, south central Kansas and southern Nevada to the Pacific coast of California. In Mexico, it seems to be limited to dry subtropical areas. In the southeastern U.S., *S. xyloni* has been largely eliminated from areas within the current range of the imported fire ant species, *S. invicta* and *S. richteri.* There is no evidence that *S. xyloni* ever inhabited any portion of Florida, and it is very rare or absent right along the Gulf Coast.

Solenopsis amblychila, **New Status**

Figs. 14, 15, 19–21

Solenopsis aurea amblychila Wheeler 1915:394. Syntype workers, queens, males. USA. Arizona. Huachuca Mts., Ramsey Canyon. (MCZ, LACM, examined.)
S. (*Solenopsis*) *xyloni amblychila*: Creighton 1930:104. Worker, queen, male.
S. aurea amblychila: Creighton 1950:230.
S. aurea: Snelling 1963:7. (In part.)

MEASUREMENTS AND INDICES: HL 1.01–1.30 (1.35), HW 0.95–1.40, SL 0.65–0.78 (0.80), EL 0.15–0.19 (0.20), PW 0.55–0.75 (0.80), AL 1.15–1.50 (1.60), CI 93–104, SI 57–72, OI 12–16. N = 24.

WORKER DIAGNOSIS. Resembling a small, yellowish *S. xyloni* and very closely resembling *S. aurea* from which only queens and major workers can be distinguished with certainty; differing from the latter as follows: head (ffv) broader, more cordate; median clypeal seta sometimes displaced off center; clypeal carinae short and blunt, or obsolete, little projecting apically, the clypeal border between them straight to weakly concave; mandibular costulae complete, 6–7 in number; eye (lv) small, ovate, greatest diameter with 8–9 (rarely 10) facets, least diameter with 6–7, at least a portion of outer ring of facets depigmented and often distorted, making the eye appear smaller; anterolateral pronotal corners (pdv) usually with small protruding bosses at angles; postpetiole 1.08–1.19× as wide as petiole.

Sculpture less pronounced than in *S. xyloni* and *S. aurea,* shinier than these species, further distinguished by the following; piligerous foveolae of head, thorax and postpetiole small and inconspicuous, rarely exceeding 0.005 mm in diameter, placed 0.08–0.20 mm apart; flange of petiolar ventral process larger, diameter of ventrally projecting portion of this flange usually greater than half length of eye, in large workers nearly as long as EL.

Pilosity of head and promesonotum less abundant than in any other fire ant, mesonotum with 8–15 erect setae.

Color reddish yellow, generally of a shade a little darker than that of *S. aurea,* and less often with posterior margins of tergites infuscated.

NOTES. Queens from the western part the range of this species may easily be distinguished from those of *S. aurea* by the same characters as the major workers, namely the broad and blunt, or missing clypeal teeth, reduced pilosity, inconspicuous piligerous punctures, and especially by their broader head, CI 108–118 (105 or less in *S. aurea*). Queens from Texas have less conspicuously broad heads, but these are still above the range of *S. aurea.*

The minor, and even submajor workers of *S. amblychila* are difficult or impossible to distinguish from those of *S. aurea,* but the former are less pilose in general, as noted in the description of the major. The consistently different queens and large majors of these forms argue for their being distinct species. There is also an ecological difference, in that in the mountains of southern New Mexico and Arizona at least, *S. amblychila* is found at elevations of about 1,500–2,500 m, while *S. aurea* is found at elevations no higher than 2000 m, and usually much below this. I have not seen any samples of the 2 species collected from exactly the same locality.

DISTRIBUTION. The types (examined) were collected in Ramsey Canyon, in the Huachuca Mountains of southern Arizona. Other specimens examined hail from the Doña Ana Mountains of New Mexico, Davis Mountains of Texas, and locations of unspecified elevation in the Mexican states of Guadalajara, Nuevo Leon, Durango, Zacatecas, and Baja California. I have not seen *S. amblychila* specimens from California, U.S.A.

Solenopsis aurea

Figs. 17, 18, 22–24

Solenopsis geminata var. *aurea* Wheeler 1906:336. Syntype workers, queen. USA. Texas. Austin. (MCZ, LACM examined); Wheeler 1908:425.

S. aurea: Forel 1909:269; Creighton; Snelling 1963:7 (in part).

S. huachucana Wheeler 1915:393. Syntype workers, queen. USA. Arizona. Huachuca Mts., Miller Canyon. (Examined.) NEW SYNONYMY.
S. (*Solenopsis*) *xyloni aurea*: Creighton 1930:103. Worker, queen, male.
S. (*Euophthalma*) *huachucana*: Creighton 1930:118. Worker, queen.

MEASUREMENTS AND INDICES: HL 1.00–1.28 (1.35), HW 0.93–1.23 (1.34), SL 0.63–0.75 (0.79), EL 0.15–0.18 (19), PW 0.55–0.75 (0.83), AL 1.10–1.49 (1.58), CI 91–100, SI 56–73, OI 13–15 (17). N = 19.

WORKER DIAGNOSIS. Resembling a small, yellowish *S. xyloni,* but differing as follows: head (ffv) narrower, weakly cordate or weakly trapezoidal (converging anteriad) as in smaller *S. xyloni*; median clypeal seta sometimes displaced off center; clypeal carinae conspicuous, projecting apically as conspicuous, isosceles-triangular teeth, the clypeal border between them straight to convex or broadly angular; mandibular costulae complete, 6–7 in number; eye (lv) small, ovate, greatest diameter with 8–9 (rarely 10) facets, least diameter with 6–7, at least a portion of outer ring of facets depigmented and often distorted, making the eye appear smaller; anterolateral pronotal corners (pdv) usually with small protruding bosses at angles; postpetiole 1.08–1.19× as wide as petiole.

Piligerous foveolae of head and thoracic dorsum 0.01–0.02 mm in diameter and mostly between 0.05–0.10 mm apart; venter of petiole with longitudinal median carina and ventral process consisting of a transparent triangular or subrectangular, jagged edged flange, diameter of ventrally projecting portion of this flange usually less than half the length of greatest diameter of eye.

Pilosity of head and promesonotum abundant, 0.08–0.30 mm in length; mesonotum with 18–30 erect setae.

Color light reddish yellow, with posterior margins of tergites brown to dark brown.

NOTES. As indicated in the discussion of *S. amblychila, S. aurea* occurs at lower elevations than the former, and indeed may be found below sea level in the deserts of California.

DISTRIBUTION. The types (examined) were collected at Austin, Texas. The range extends west to inland California and south into northern Mexico, mainly in desert and dry grassland regions.

GAYI SUBCOMPLEX

Solenopsis gayi

Figs. 36, 37, 48, 49

Myrmica gayi Spinola 1851:242. Syntype workers, queen, male. CHILE. Santiago. (Not examined.)
Pogonomyrmex gayi: Mayr 1868:170.
Solenopsis gayi: Mayr 1870:971–972. Worker; Snelling and Hunt 1975:84–85. Worker, queen, male (illustrated). (Various Chilean localities, examined.)
Solenopsis geminata gayi: Emery 1895.
Solenopsis (*Solenopsis*) *gayi*: Creighton 1930:48–51.
Solenopsis gayi var. *fazi* Santschi 1923. Syntype workers, queens. CHILE. Santiago. (NMB, examined.) *Solenopsis gayi* var. *fazi*: Creighton 1930. (Synonymy by Snelling and Hunt, 1975.)

MEASUREMENTS AND INDICES: HL 1.00–1.23, HW 0.94–1.26, SL 0.73–0.86, EL 0.15–0.20, PW 0.51–0.69, AL 1.24–1.51, CI 94–103, SI 68–80, OI 14–16. N = 10.

WORKER DIAGNOSIS. The smallest South American fire ant and the only one found in Chile, distinguished as follows: head (ffv) subrectangular, except in largest workers in which it may be convergent anterior to eyes; sides straight to weakly convex; posterior border straight or with a broad, shallow concave median impression, concavity occupying nearly entire breadth of the posterior borders; median clypeal tooth lacking; clypeal carinae conspicuous, close-set, projecting apically as long, blunt teeth; clypeal border between carinal teeth strongly concave; distance between teeth a little over ½ × distance between apices of frontal lobes (about ¾ this distance in most species outside *gayi* subcomplex); mandibles straight near base, then curving mesad as in media workers of *S. geminata*; mandibular costulae 6–7 in number, complete and well developed; eye (lv) ovate, greatest diameter with 8–9 facets, least diameter with 6–7 (facet count 40 or less in minors); scapes (ffv) in majors failing to reach rear border of head by 3–5 × greatest scape width, and even in small minors, distance between tip of scape and occipital corner about 1–2 × apical width of scape (scape reaching or exceeding posterior border in minors of all other species except *xyloni* complex), stated otherwise, CI varied less with size than in other species; anterolateral pronotal corners (pdv) rounded; metanotal impression conspicuous, but shallow and weakly sculptured compared to other species besides *S. bruesi*; propodeal profile with anterior declivity obsolete, grading insensibly into weakly convex dorsum, the latter ranging from distinctly sloped to little or not at all sloping posteriad; dorsal face of propodeum meeting rear face through rounded-off obtuse to right angles; petiolar peduncle a little shorter to slightly longer than base of node; postpetiolar node in profile lower than petiole, globular; outline of postpetiolar node (pdv) globular and little or not at all wider than petiole.

Piligerous foveolae of head and thoracic dorsum small, 0.003–0.005 mm in diameter; sculpture of mesometapleuron (lv) normal or sometimes reduced, with longitudinal rugae and interstitial punctation largely obsolete; area surrounding propodeal spiracle shining, unsculptured; declivous face of propodeum with transverse striae below, contiguous with those of metapleuron; petiolar peduncle and base of node weakly areolate; venter of petiole with longitudinal median carina and ventral process consisting of at most a small protuberance; petiolar and postpetiolar nodes largely unsculptured, shining and globular as in *S. virulens,* except for faint transverse rugae at base of rear face of postpetiole in some specimens.

Pilosity of head and promesonotum as in *S. aurea.*

Color uniform dark reddish brown with the gaster slightly darker; many specimens have at least part of the clypeus, frons, sides of head in front of eyes, and a triangular area that would have its corners approximately at the positions of the ocelli if these were present, lighter reddish or even yellowish; the lightest specimens may have a distinct yellowish brown spot on the first tergite.

NOTES. Snelling and Hunt (1975) state that *S. gayi* "is one of the commonest ants in Chile, and is the most widely distributed." In southern Peru, *S. gayi* is sympatric with *S. bruesi,* but is apparently limited to low elevations (up to 500 m).

DISTRIBUTION. The types of *S. gayi* (not examined, but certainly belonging to this, the only fire ant species in Chile) were described from Santiago, Chile. It occurs

from as far south as Malleco province, Chile north to southern Peru. I have seen a sample from Villavicencio, Meta, Colombia, which may represent an introduction.

Solenopsis bruesi, **New Status**
Figs. 34, 35, 46, 47

Solenopsis (*Solenopsis*) *gayi bruesi* Creighton 1930:52–53. Syntype workers. PERU. Chosica Canyon (near Lima). C. T. Brues. (MCZ, LACM, examined.)

MEASUREMENTS AND INDICES: HL 1.00–1.47, HW 0.92–1.47, SL 0.73–0.98, EL 0.16–0.24, PW 0.51–0.80, AL 1.16–1.73, CI 91–106, SI 66–83, OI 14–19. N = 16.

WORKER DIAGNOSIS. Closely resembling a large, reddish *S. gayi* in morphology, with the following characteristics like those of the latter: head (ffv) subrectangular, except in largest workers in which it may be convergent anterior to eyes; sides straight to weakly convex; posterior border straight or with a broad, shallow concave median impression, concavity occupying nearly entire breadth of the posterior borders; median clypeal tooth lacking; clypeal carinae conspicuous, close-set, projecting apically as long, blunt teeth; clypeal border between carinal teeth strongly concave; distance between teeth a little over ½× distance between apices of frontal lobes (about ¾ this distance in most species outside *gayi* subcomplex); scapes (ffv) short in majors, failing to reach rear border of head by 3–5× greatest width of scape, and even in small minors, distance between tip of scape and rear corner of head about 1–2× scape widths (scape reaching or exceeding posterior border in minors of all other species except *xyloni* complex), stated otherwise, CI varies less with size than in other species; outline of postpetiolar node (pdv) globular and little or not at all wider than petiole.

Differing from *S. gayi* in the following: larger, about the size of *S. invicta*; blade of mandible broader, mandibular costulae finer and more numerous, 8–9 in number, complete and well developed; eye (lv) larger, greatest diameter with 9–12 facets, least diameter with 7–8 (facet count 50 or more in minors).

Piligerous foveolae of head and thoracic dorsum smaller than those of *S. gayi,* rarely in excess of 0.003 mm in diameter; all other sculpture reduced, often lacking altogether, yielding a generally quite shiny ant.

Pilosity of head and promesonotum of the usual sort for the *saevissima* complex, though a little less abundant than in other species, mesonotal dorsum with about 20 erect setae (25 or more in most other species).

Color uniform reddish brown to light reddish, with the gaster slightly darker; triangular area that would have its corners approximately at the positions of the ocelli if these were present, distinctly darker than surrounding area (lighter reddish or yellowish in *S. gayi*).

NOTES. Creighton described *S. bruesi* from media workers, stating that their features "might be considered sufficient to entitle it to specific status, [but] the question turns upon the character of the [as yet uncollected] sexual forms." While the latter remain unknown, the major worker specimens collected by Weyrauch leave no doubt in my mind that this is a distinct species. The majors resemble nothing so much as submajors of *S. geminata* from which all the sculpture has been polished off. From label information, we gather *S. bruesi* occurs in wild areas, including sand deserts and canyons, but also occurs in urban areas.

DISTRIBUTION. The types (examined) came from Chosica Canyon, (near Lima), Peru. Additional localities are Trujillo, and others in the vicinity of Lima.

SAEVISSIMA COMPLEX

This complex contains 2 subcomplexes. While it is fairly certain that the *saevissima* subcomplex is monophyletic, this is less certain for the *electra* subcomplex. As a complex, all the species are characterized by their cis-Andean South American distribution (except *S. weyrauchi* may be found in the Pacific drainage), polymorphism of the workers, long scapes of the minor, weak sculpture, and a small or absent ventral process on the petiolar pedicel.

The *electra* subcomplex contains two species, *S. electra* and *S. pusillignis,* found in the dry western portion of South America east of the Andes. Both have small sexual forms, and the head shape of the majors is similar. They are described near the end of this paper.

The remaining species form the *saevissima* subcomplex. They inhabit grasslands and forest openings (usually near water, often in seasonally flooded habitats) in tropical to warm temperate lowland South America. An interesting exception is *S. weyrauchi* which lives in the cool bunch grass habitats of the Andean uplands of Peru. These are relatively large species, with long scapes, and in every case known, their venoms cause pustules on the skin of human victims of their stings. *S. invicta* is intermediate in size and sculpture between the "extreme" species of the subcomplex, *S. saevissima* and *S. macdonaghi,* and is used as the "standard" to which most other species are compared in the following treatment. The parasites of the *S. daguerrei* group all live with species of the *saevissima* subcomplex, and are apparently derived from it.

SAEVISSIMA SUBCOMPLEX

Solenopsis invicta

Figs. 50, 51, 56, 57

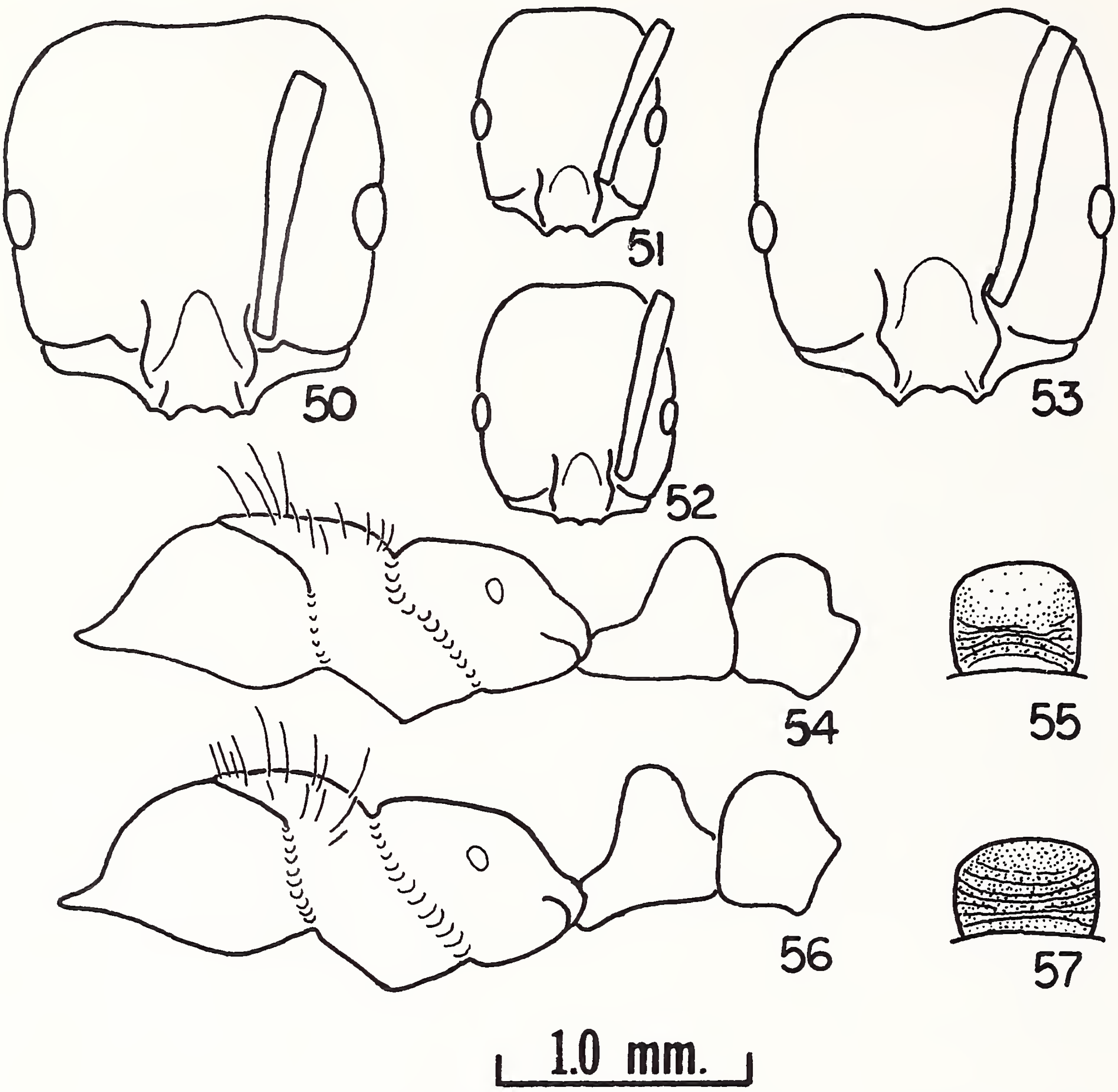
Solenopsis saevissima saevissima cline *S. saevissima richteri* ("light red phase" and probably also "subsp. *electra*"): Wilson 1952:65. Workers from USA. Alabama, Mississippi. (MCZ, examined.) (Synonymy by Ettershank, 1966:136.)

S. invicta Buren 1972:9. Worker, queen, male. (This name was misspelled as "*invica*" at the head of the species description in Buren's paper, but it is clear from the rest of the paper and the etymology of the name, not to mention a huge body of subsequent usage, that *invicta* was the intended spelling.)

S. quinquecuspis: Buren 1972:17–19. (Numerous workers in WFB, examined.) MISIDENTIFICATION.

(But not *Solenopsis pylades* var. *quinquecuspis* Forel 1913:224, which is a valid, distinct species.)

S. saevissima electra var. *wagneri* Santschi 1916:380. Syntype worker. ARGENTINA. Santiago de Estero. Near Icano. Wagner. (NMB, examined. Other specimens probably exist in the Paris Museum, but were not examined.) NOT AVAILABLE; Santschi 1923:266. Creighton, 1930:94. (In part only, since Santschi's types were included among the localities.)



Figs. 50–53. South American *Solenopsis* heads, full face view. 50–51. *S. invicta*; major and minor. 52–53. *S. richteri*; minor and major.

Figs. 54–57. South American *Solenopsis* trunk profiles and postpetiole rear views of major workers. 54–55. *S. richteri*. 56–57. *S. invicta*.

NOTE: Though it has priority over Buren's name, *wagneri* is not an available name, as it has never been used above infrasubspecific rank. Uses of the name since Santschi have not been associated with specimens and thus are, in effect, nomina nuda.

MEASUREMENTS AND INDICES: HL 1.00–1.47 (1.49), HW 0.90–1.42 (1.49), SL 0.80–1.06, EL 0.18–0.26 (0.27), PW 0.55–0.90, AL 1.26–190, CI 89–99 (101), SI 70–92, OI 15–18 (19). N = 40.

WORKER DIAGNOSIS. Head (ffv) subquadrate to weakly cordate (occasionally broader and more cordate in particularly large individuals), with sides convex; posterior border with a shallow concave median impression, the concavity about 1.5× or more as wide as distance between apices of frontal lobes; median clypeal tooth well-developed, usually sharp and about 0.5× as long as lateral teeth, sometimes

displaced off center; median clypeal seta conspicuous, arising at or near apex of median tooth; clypeal carinae conspicuous, projecting apically as acuminate, triangular teeth, or curved mesad and faintly falcate; space between clypeal carinae concave, except near base of median tooth; mandibles with the usual curvature; mandibular costulae mostly obsolete except distally and near base along outer border, rarely one or more of the median intercostular furrows extends length of mandible; eye (lv) ovate, greatest diameter with 11–14 (rarely less) facets, least diameter with 8–10, often outer ring of facets depigmented, especially anteriorly; distance between tip of scape and occipital corner about 0.08–0.15× scape length in major workers, (ffv) in smallest workers scape apex easily reaches or slightly exceeds posterior border; anterolateral pronotal corners (pdv) rounded to weakly angular, especially in smaller workers, but only very rarely with a protruding humeral boss; anteroventral border of mesopleuron with a seam-like flange separating its lateral portion from the ventral concavity in which the procoxa fits at rest, though often this seam obsolete anteriorly or absent altogether; metanotal impression conspicuous; propodeal profile with anterior declivity short, convex, set off from propodeal dorsum by a rounded angle; propodeal dorsum weakly convex, descending through rounded angles to declivous face, or rarely forming a continuous convexity with the declivous face, in which case both surfaces more rounded than usual; petiolar peduncle notably to slightly shorter than base of node; postpetiolar node in profile lower than petiole, globular, sometimes with dorsoposterior face a little more convex than anterior face, outline of postpetiolar node (pdv) subrectangular to subtrapezoidal, with dorsal outline weakly convex, and lateral faces straight, parallel to convergent ventrad; postpetiole 1.04–1.15× as wide as petiole.

Piligerous foveolae of head and thoracic dorsum typically small, round and inconspicuous, mostly 0.003–0.005 mm in diameter, but occasionally up to 0.01 mm and slightly elongate, especially in darker color variants from southeastern part of range (SE Brazil, Uruguay, Argentina); sculpture of mesometapleuron (lv) consisting of fine longitudinal striae or rugose striae, often with interstitial punctation or areolation; sculpture often weakened or obsolete on mesial and/or anteroventral portion of mesopleuron; surface of mesopleural marginal flange, when present, roughened; dorsum of propodeum unsculptured; area surrounding propodeal spiracle usually unsculptured, except frequently some semicircular rugae behind, and rarely above, spiracle, but these separated from spiracle by a smooth, shiny area; declivous face of propodeum with transverse striae contiguous with those of metapleuron; petiolar peduncle, and sometimes base of node, weakly areolate; venter of petiole with longitudinal median carina and ventral process obsolete or consisting of a small truncate projection; petiolar node largely unsculptured except piligerous foveolae, and perhaps a few shallow longitudinal furrows; dorsum of postpetiole unsculptured other than piligerous foveolae, or rarely weakly transversely striate-punctate; posterior face of postpetiole mostly shiny near top, transversely rugose or punctate-rugose on lower ⅔ or more.

Pilosity of head and promesonotum abundant, 0.08–0.33 mm in length; 2–8 erect setae also present on mesopleuron and 1 or 2 on metapleuron, gaster pilosity normal.

Color variable, though generally fairly consistent within a colony; bicolored, with head and thorax ranging from concolorous yellowish-red to dark reddish brown, gaster brown with a large spot the color of the foreparts of tergite I to nearly con-

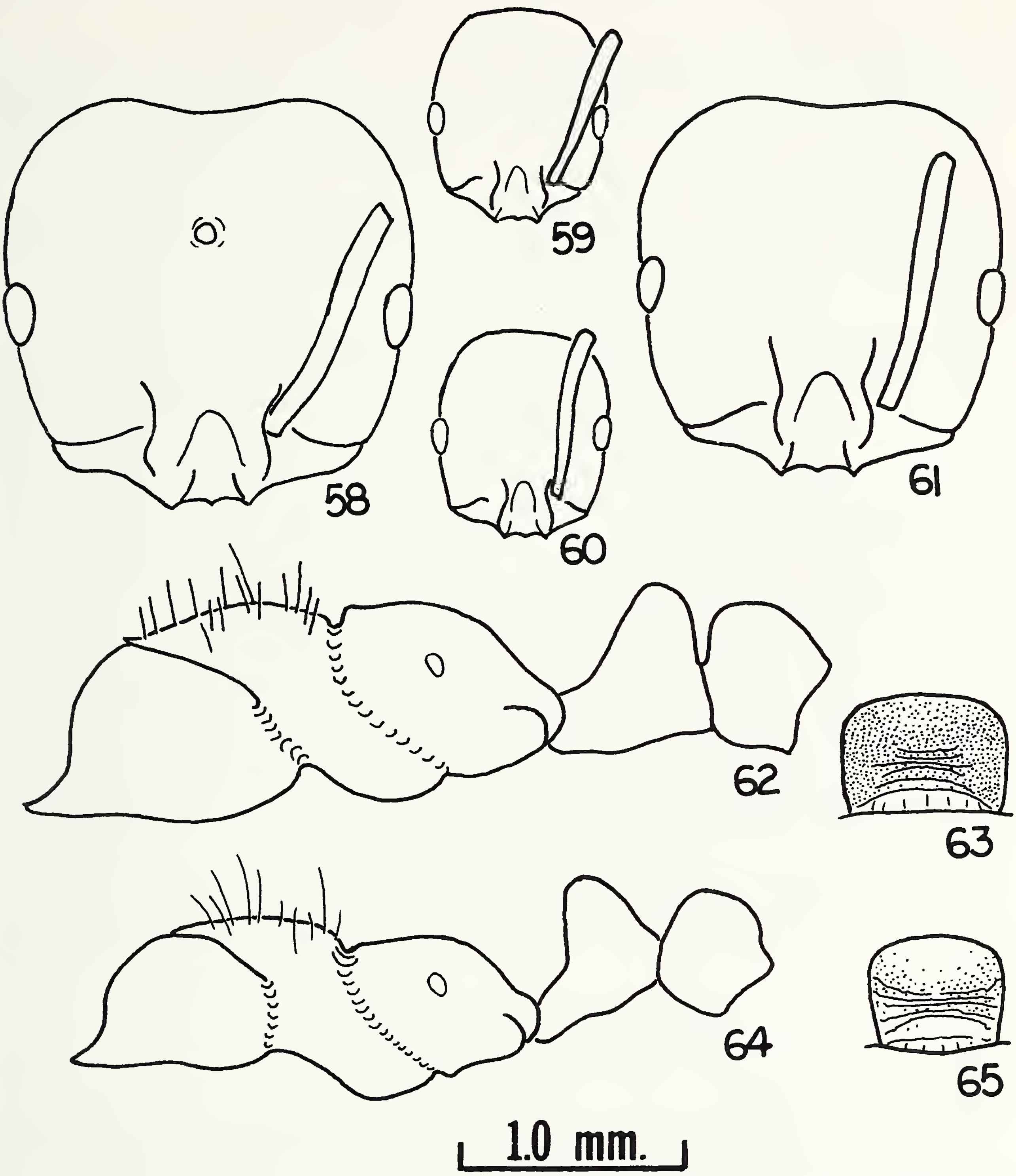
colorous brownish black; head of darker variants often concolorous except for dark frontal streak (not usually conspicuously lighter near base of mandibles and on clypeus as in the related *S. quinquecuspis*); frontal triangle and narrow median impression behind it notably darker than surrounding area in most specimens of all sizes, except in the brightest red specimens from the northern and western parts of the range. Smaller workers tend to be colored darker than larger workers of the same colony. The darkest color variants are most common from southeastern Brazil to east-central Argentina (but can be found locally as far west and north as Mato Grosso), interspersed among redder colonies, or in more uniformly dark local demes. A pale, honey colored form occurs locally in the pantanal of Mato Grosso, and rarely elsewhere.

NOTES. This is the infamous red imported fire ant of the southeastern U.S.A. The North American population appears to have originated in the Paraguay River drainage of South America, where at least the majority of ants among the South American *S. invicta* thus far studied most closely resemble the North American population in venom chemistry (Vander Meer, unpubl. data), allozyme allele frequencies (Ross and Trager, 1991) and color and morphology (this study). The area in question includes southern Mato Grosso and Mato Grosso do Sul, Brazil, all of Paraguay and northern Argentina. Buren's (1972) selection of Cuiabá as the type locality is thus close to the mark in terms of selecting an area in South America from which the specimens would be representative of both the North American and South American populations. However, in terms of shipping routes and practices in the late 1930's, I believe it more likely that *S. invicta* arrived with cattle from northern Argentina or Paraguay.

Of the 2 imported fire ant species, *S. invicta* has been much more successful in North America than *S. richteri,* as evidenced by the now much retracted range of the latter there. The hybrid population resulting from the crossing of these two species (and subsequent reproduction within the hybrid population) has also retreated in the face of the spread of *S. invicta,* though the mechanism (competitive displacement, genetic swamping, other?) is unclear. See the notes on *S. richteri* for further information relevant to hybrid imported fire ants.

In the light of the fertility and evident viability of the hybrid, one may legitimately question my maintenance of these forms as distinct species. I base this upon the behavior of the species in South America. In the small area in Argentina where they are sympatric, available evidence of introgression between *S. invicta* and *S. richteri* indicates that it occurs only at a very low rate (Ross and Trager, 1991). Several features of the North American populations of both species indicate that they originated far from the zone of natural sympatry in South America, and it is not unreasonable to hypothesize that the North American populations of *S. invicta* and *S. richteri* came from populations that either had lost or never had whatever isolating mechanisms exist in the area of sympatry.

DISTRIBUTION. The types (examined) are from Cuiabá, Mato Grosso, Brazil. In North America, *S. invicta* occurs from the Carolinas to Florida west to Texas. Isolated populations have been found somewhat to the north of this area, and have also been found in New Mexico, Arizona and California, where they arrived with sod or nursery stock from the southeast. These outlier populations were quickly eliminated shortly after their discovery. In South America, *S. invicta* is found from northern Mato Grosso west to Peru and Bolivia, south to Santiago del Estero and



Figs. 58–61. South American *Solenopsis* heads, full face view. 58–59. *S. macdonaghi*; major and minor. 60–61. *S. interrupta*; minor and major.

Figs. 62–65. South American *Solenopsis* trunk profiles and postpetiole rear views of major workers. 62–63. *S. macdonaghi*. 64–65. *S. interrupta*.

Santa Fé provinces in Argentina and northeast through Uruguay and southern Brazil to São Paulo state.

Solenopsis interrupta
Figs. 60, 61, 64, 65

Solenopsis saevissima var. *interrupta* Santschi 1916:397. Syntype (?) workers (see discussion). ARGENTINA. La Rioja. Bajo Hondo. (USNM, examined; NMB, not examined.)

S. (*Solenopsis*) *saevissima interrupta*: Creighton 1930:89. (In part.)
S. interrupta: Wilson 1952:61. (In part.)
(*S. interrupta*: Buren 1972:22 is in the synonymy of *S. macdonaghi.* Buren recognized the true *S. interrupta* as a distinct species, but assigned the name incorrectly (Buren, pers. comm.).)

MEASUREMENTS AND INDICES: HL 1.19–1.60, HW 1.05–1.53 (1.61), SL 0.90–1.15, EL 0.20–0.28, PW 0.63–0.90 (0.95), AL 1.35–1.89 (2.00), CI 88–99 (101), SI 66–90, OI 15–19. N = 22.

WORKER DIAGNOSIS. Larger, more yellowish or amber-colored than *S. invicta,* differing additionally as follows: Head (ffv) weakly cordate to strongly cordate, with sides weakly to notably convex; posterior border with a concave median impression about as in *S. invicta,* but tending to be a little narrower and deeper, the concavity less than 1.5× distance between apices of frontal lobes; mandibles with the usual curvature; mandibular costulae usually complete and close set, yielding a silky sheen to the mandibular upper surface (rather than highly polished mesial region typical in *S. macdonaghi* and most common in *S. invicta*), costulae rarely partly obsolete mesially; anterolateral pronotal corners (pdv) usually weakly angular, protruding humeral bosses lacking or at most feebly protruding; propodeal profile with anterior declivity of most workers straight, sloped backward, set off from propodeal dorsum by a distinct angle; propodeal dorsum weakly convex, sloping to the rear, descending through rounded angles to declivous face, never forming a continuous convexity with the declivous face; postpetiolar node in profile lower than petiole, globular, sometimes with dorsoposterior face a little more convex than anterior face, outline of postpetiolar node (pdv) subtrapezoidal, with dorsal outline weakly convex, and lateral faces straight or concave, slightly to notably convergent ventrad.

Sculpture as in less heavily sculptured series of *S. invicta,* in particular, *S. interrupta* tends to have the postpetiolar rear face weakly transversely rugose with interrugal punctation weakly developed, this sculpture rarely reaching postpetiolar dorsum except in some large workers.

Vestiture not appreciably different from that of *S. invicta,* but finer and much more variable in length than in typical specimens of the otherwise somewhat similar *S. macdonaghi.*

Two more or less distinct color forms of *S. interrupta* occur. The most common form has the head predominantly bright reddish or amber yellow; median frontal impression sometimes darkened as in *S. invicta,* but more often not; thorax weakly infuscated dorsally, appendages and rear portion of the head somewhat darker; gaster dark brown with gaster spot occupying at least ⅔ of first tergite, this also true of median and many small workers (spot rarely occupies more than ½ to ⅗ of tergite in *S. invicta* and obsolete on smaller workers). A less common form, but one predominating in the vicinity of Santa Cruz, Bolivia and occurring less frequently elsewhere is colored uniform dusky yellowish brown dorsally, fading to yellower on the anterior half of the head, pleura and coxae; median frontal dark streak poorly defined; gaster spot only slightly lighter than remainder of gaster, occupying only about half the tergite and fading gradually into darker area, or even obsolescent.

NOTES. See notes on *S. macdonaghi* for comments on separating these two large and generally brightly colored species.

The darker color form may be difficult to separate from sympatric *S. invicta,* but the latter generally has a more rectangular postpetiolar node, and has a rather distinct median frontal dark streak surrounded by a notably lighter and yellower surrounding region of the frons and clypeus, at least.

Occasional colonies have weakly developed polymorphism as in polygyne colonies of *S. invicta.* Their smaller size and somewhat darker color will probably render them impossible to identify by any other than the most experienced collector of fire ants, unless one resorts to biochemical genetic characters (Ross and Trager, 1991). Polygyny is suspected, but not confirmed in these colonies.

Within the *saevissima* subcomplex, this is certainly the most xerophilic species, and may be found together with *S. electra* in at least the eastern portion of the deserts of northern Argentina and in the dry Andean foothills.

There is some question about the type locality of *S. interrupta.* The original description states that the specimens were from "Bajo Hondo, Argentina," but there are two widely separated localities by this name in Argentina. One is in La Rioja province, well within what I understand to be the normal range of this species, and the other in a portion of Buenos Aires province inhabited, to my knowledge, by only 2 fire ant species, namely *S. quinquecuspis* and *S. richteri.* I have not examined types, but a series in USNM has the same locality and collector data, and may be from the same colony. They appear to be typical western Argentine *S. interrupta,* and since the collector (Carette) travelled widely in that region as well as in Buenos Aires, I think it safe to assume that the sample was collected in La Rioja.

DISTRIBUTION. The types (not seen, but studied by W. F. Buren) were collected in Bajo Hondo, La Rioja, Argentina. (Mistakenly, I believe, listed as Bajo Hondo, Buenos Aires by Santschi and Creighton. See above.)

The distribution of *S. interrupta* has its southern extremes in Cordoba and Mendoza provinces in west central Argentina, and extends north along the base and foothills of the Andes well into Bolivia.

Solenopsis macdonaghi, New Status

Figs. 58, 59, 62, 63

Solenopsis saevissima var. *macdonaghi* Santschi 1916:397. Syntype workers, queens. ARGENTINA. Entre Rios. Estación Sosa. MacDonagh. (NMB, examined.)

S. geminata pylades: Bruch 1916:313. (Not examined.) (Synonymy by Emery, 1925.)

S. (*Solenopsis*) *saevissima interrupta*: Creighton 1930:89. (In part.) MISIDENTIFICATION.

S. interrupta: Wilson 1952:61. (In part.) MISIDENTIFICATION.

S. interrupta: Buren 1972:22. MISIDENTIFICATION.

(But not *Solenopsis saevissima* var. *interrupta* Santschi 1916:397, which is a valid, distinct species.)

MEASUREMENTS AND INDICES: HL 1.05–1.69 (1.75), HW 0.93–1.73 (1.80), SL 0.80–1.15, EL 0.20–0.33 (0.35), PW 0.58–1.15, AL 1.26–2.10 (2.21), CI 90–102 (103), SI 63–90, OI 16–20. N = 23.

WORKER DIAGNOSIS. Most closely resembling *S. interrupta*; larger, more reddish than most *S. invicta,* differing additionally as follows: Head (ffv) broad (often slightly broader than long) cordate, with sides convex; posterior border with a concave

median impression, the concavity about as wide as distance between apices of frontal lobes; median ocellus usually conspicuous and with a clear lens in large and even in some smaller specimens; mandibular costulae mostly obsolete except distally and near base along outer border, less often (especially in series from Paraguay and Bolivia) costulae more or less complete; pronotal profile more arched than in other species; anterolateral pronotal corners (pdv) rounded, weakly angular in smaller workers, but lacking protruding bosses; metanotal impression deep; anterior declivity of propodeum straight, higher than in other species, set off from propodeal dorsum by a more or less rounded angle; anterior portion of propodeal dorsum flat to weakly concave (upturned to meet anterior angle), posterior portion convex and sloping through an even convexity to a low posterior face, or the latter set off by a rounded broadly obtuse angle; petiolar peduncle notably shorter than base of node, the node appearing a little thicker basally than in other species; postpetiolar node (pdv) broad, subrectangular; with dorsal outline weakly convex, lateral faces straight, parallel.

Piligerous foveolae of head and thoracic dorsum typically round and more conspicuous than in *S. interrupta,* about 0.01 in diameter, occasionally larger and slightly elongate; rear face of postpetiole usually lacking or with only very weak transverse rugae except near base, uniformly and densely punctate, the punctation usually extending onto dorsum of postpetiole.

Pilosity of head and promesonotum abundant, 0.08–0.33 mm in length as in other species, but in most specimens, the majority of setae are of more or less uniform length (0.15–0.25 mm); setae flatter at base, redder in color, and less curved than is typical of other species.

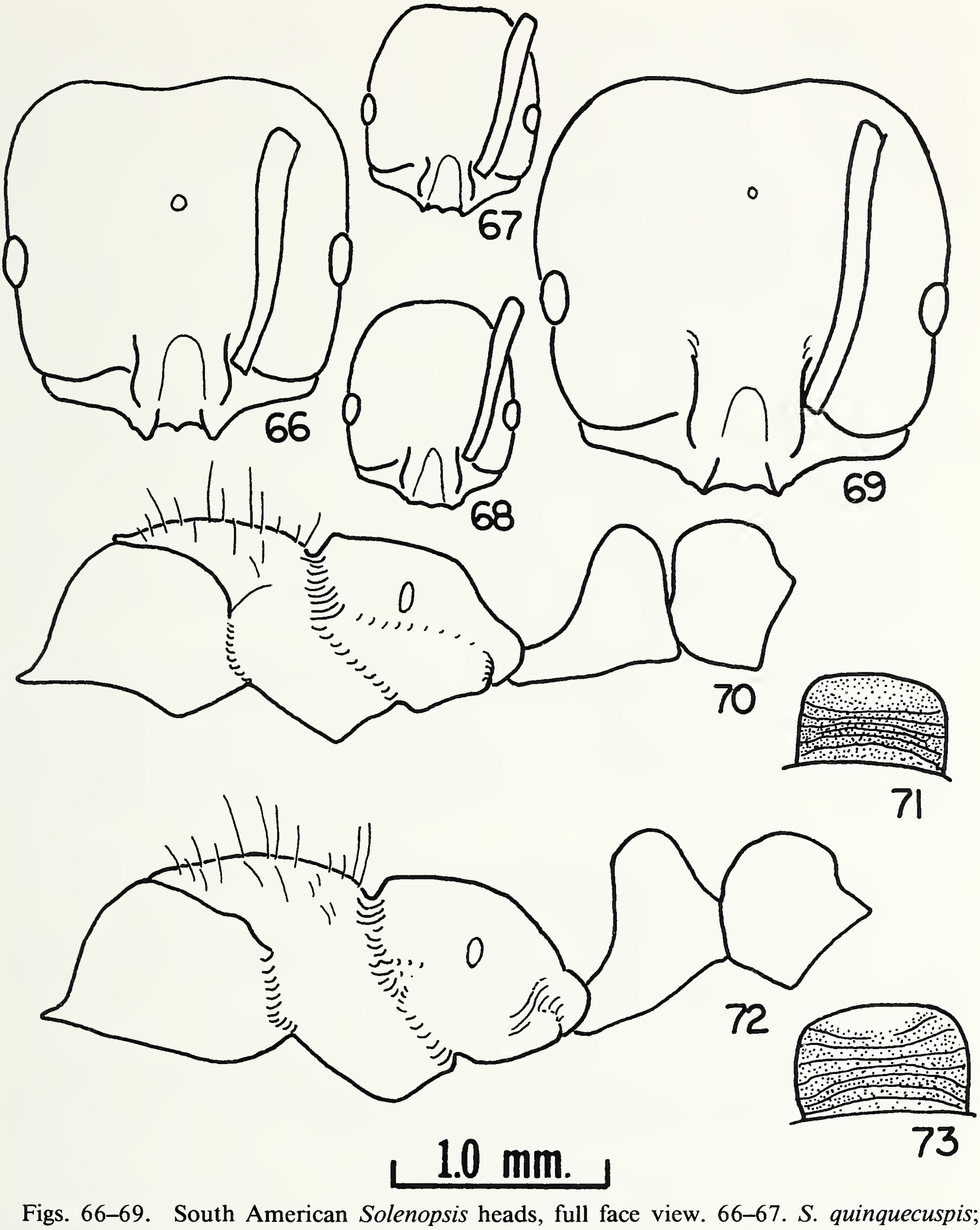
Color reminiscent of that of *S. interrupta,* but usually lacking faint infuscation of head and thorax and of a slightly deeper hue, thus appearing redder in the field, this distinction elusive in pinned specimens. Occasional colonies are darker, closely resembling *S. quinquecuspis.*

NOTES. As indicated in the synonymy, this species has been thought by some authors to be the typical *S. interrupta,* or at least part of the normal variation of the latter. *S. macdonaghi* is more eastern in distribution, is redder in color, has mesially obsolete mandibular costulae, usually bears a well developed median ocellus (occasionally even on submajors), has the thoracic dorsum covered with straight reddish pilosity of nearly uniform length on many specimens, and the rear face of the postpetiole is broad and subquadrate and bears dense, punctulate sculpture over all or nearly all of its surface.

Though largely allopatric, *S. interrupta* and *S. macdonaghi* may be found together at least in the vicinity of Cochabamba, Bolivia. Although the Bolivian population often has complete mandibular costulae, the more uniform pilosity length, well-developed ocellus and broader, more sculptured postpetiole of *S. macdonaghi* will distinguish major workers of this population.

The queen of this species may also be recognized by its broad head. The CI of 5 queens measured at random was 101–104, while queens of all other species in the *S. saevissima* complex (including *S. interrupta*) had CI $\leq$ 101.

DISTRIBUTION. *S. macdonaghi* is characteristic of the vast floodplain of western Uruguay and "mesopotamian" eastern Argentina, and there are a few records from Paraguay. The population at Cochabamba, Bolivia is disjunct and probably introduced.



Figs. 66–69. South American *Solenopsis* heads, full face view. 66–67. *S. quinquecuspis*; major and minor. 68–69. *S. megergates*; minor and major.

Figs. 70–73. South American *Solenopsis* trunk profiles and postpetiole rear views of major workers. 70–71. *S. quinquecuspis*. 72–73. *S. megergates*.

Solenopsis megergates, new species
Figs. 68, 69, 72, 73

MEASUREMENTS AND INDICES: HL 1.04–1.75, HW 0.90–1.79, SL 0.88–1.30, EL 0.18–0.27 (0.29), PW 0.53–1.10, AL 1.12–2.33, CI 87–106, SI 71–98, OI 14–18. N = 20.

HOLOTYPE MEASUREMENTS: HL 1.69, HW 1.71, SL 1.26, EL 0.26, PW 1.05, AL 2.32, CI 101, SI 74, OI 15.

WORKER DIAGNOSIS. A large, brown species, likely to be confused in appearance only with *S. quinquecuspis,* and in size with *S. macdonaghi,* distinguished as follows (compared to *S. quinquecuspis*): head broader than long in most large majors (ffv), cordate, with sides convex; posterior border with a concave median impression, the concavity shallower than in *S. quinquecuspis,* but about 1.1–1.4× as wide as distance between apices of frontal lobes as in that species; mandibular costulae sometimes obsolescent mesially but most often extend entire length of mandible and broaden mesially; eye (lv) appears and is often, in fact, smaller and less elongate, but with about the same number of somewhat smaller ommatidia, than in *S. quinquecuspis*; anterolateral pronotal corners (pdv) rounded to weakly angular, tending toward weakly angular in smaller workers, with anterolateral ridge-like bosses; propodeal profile most often a continuous convexity, with anterior and posterior declivities indistinct, less often the faces distinct and separated by rounded angles as in *S. quinquecuspis*; form of petiole and postpetiole as in *S. quinquecuspis.*

Piligerous foveolae of head and thoracic dorsum round, conspicuous, about 0.01 mm or more in diameter; sculpture otherwise as in *S. invicta,* i.e., posterior face postpetiole transversely rugose on lower half to ¾, with weak interrugal punctation, sculpture not usually extending onto dorsum.

Vestiture of the normal sort for the complex; abundant, highly varied in length on head and especially on thoracic dorsum, the longer setae curved.

Weakly bicolored, head, thorax, gaster spot and appendages uniform reddish brown; dorsum of petiole and postpetiole, and remainder of gaster darker brown; median frontal furrow not distinctly colored or at most faintly darker than remainder of frons.

NOTES. *S. megergates* has the largest workers of any fire ant species, hence the name, which is Greek for "large worker." The queens are not especially large, and cannot be readily distinguished from some *S. quinquecuspis* or *S. invicta.*

DISTRIBUTION. *S. megergates* is known only from southeastern Brazil, including the states of Paraná, Santa Catarina and Rio Grande do Sul. The type series was collected 4 km N of Curitiba, Paraná, Brazil.

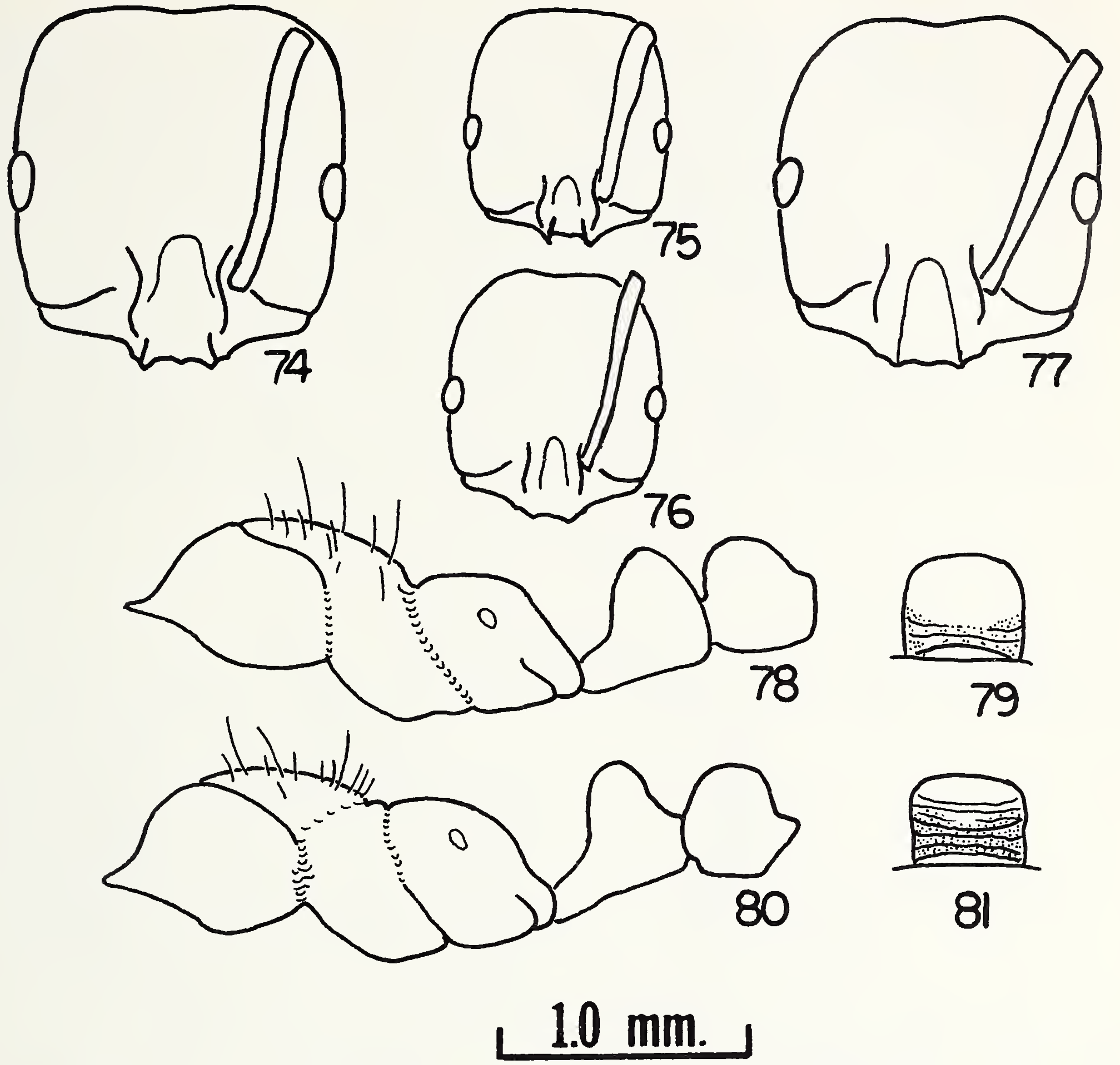
TYPE DEPOSITION. The holotype worker and 20 paratypes will be placed in MZSP. 52 remaining paratypes and numerous other specimens will be divided between AMNH, BMNH, FSCA, LACM, MCZ and MZSP.

Solenopsis pythia
Fig. 83

Solenopsis pythia Santschi 1934:30. Holotype queen. ARGENTINA. Misiones. Loreto. A. A. Oglobin. (NMB, examined.)
Solenopsis (*Solenopsis*) *pythia*: Wilson 1952:61. Queen.

MEASUREMENTS AND INDICES: HL 1.00–1.20, HW 0.91–1.14, SL 0.76–0.90, EL 0.17–0.23, PW 0.55–0.65, AL 1.22–1.47, CI 87–96, SI 77–91, OI 16–20. N = 21.

WORKER DIAGNOSIS. A species virtually indistinguishable from media and small major workers of the small, brown variety of *S. saevissima* found in southeastern

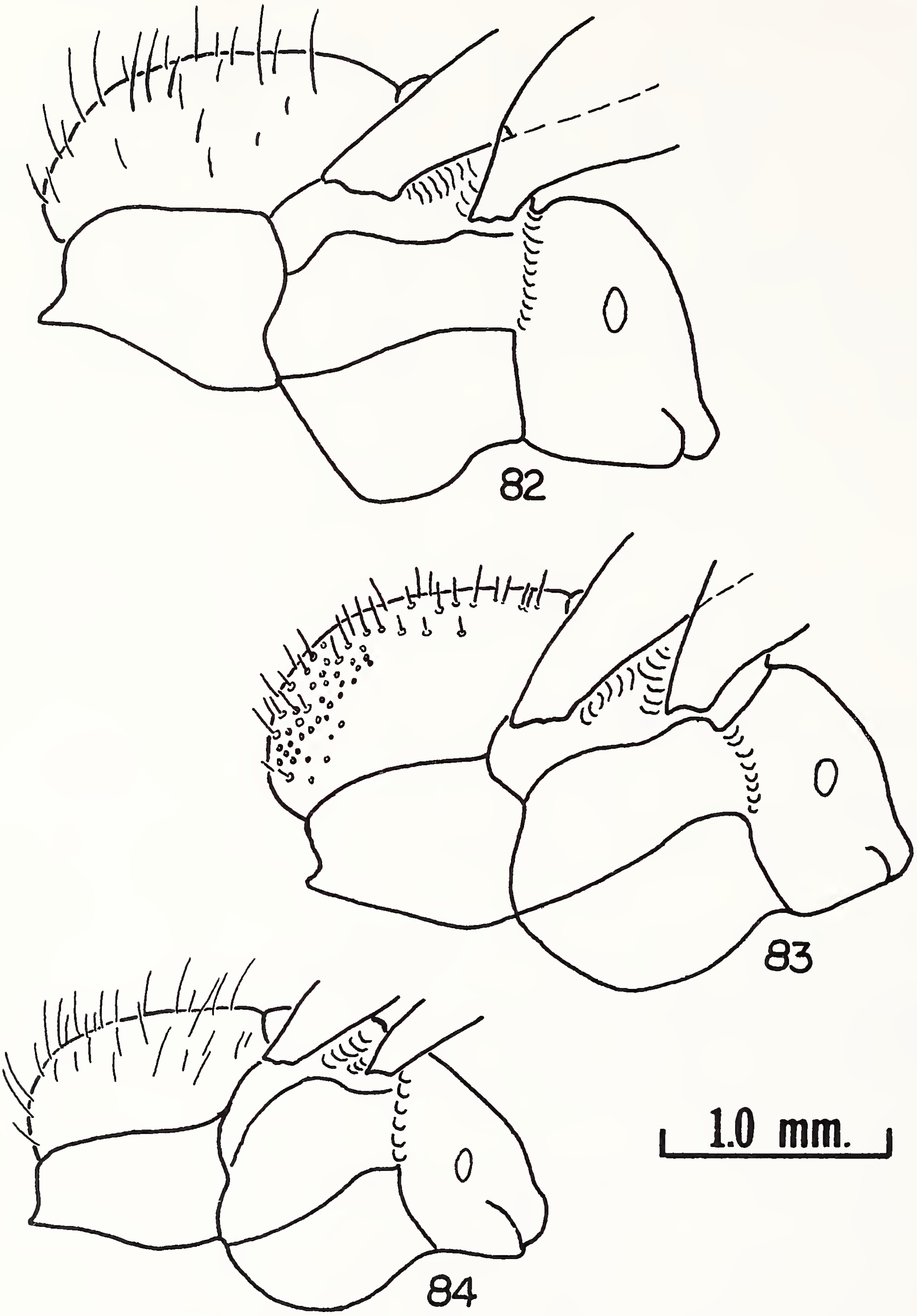


Figs. 74–77. South American *Solenopsis* heads, full face view. 74–75. *S. saevissima*; major and minor. 76–77. *S. weyrauchi*; minor and major.

Figs. 78–81. South American *Solenopsis* trunk profiles and postpetiole rear views of major workers. 78–79. *S. saevissima*. 80–81. *S. weyrauchi*.

Brazil (var. *perfida*), some larger workers have conspicuous piligerous foveolae many of which are 0.01 mm or more in diameter on the head and pronotum (less than 0.01 mm in *S. saevissima*). See queen diagnosis for more certain separatory characters.

QUEEN DIAGNOSIS. In color and proportions, resembling a small version of Amazonian *S. saevissima,* but differing conspicuously in pilosity and sculpture: pilosity of entire dorsum relatively uniform in length, 0.15–0.20 mm (many setae over 0.30 mm in all other species), to slightly longer on head, pilosity dense, arising from conspicuous foveolae 0.01–0.15 mm in diameter even on gaster (0.005–0.01 in other species, even smaller on gaster); interfoveolar spaced on much of head (especially frons) and anterior pronotum of most specimens sculptured with fine, weak, confused rugosity (head lacking such sculpture in other species, or at most with faint rugosity on frons); pleura sculptured with longitudinal, slightly irregular striae (pronotum and pleura unsculptured other than piligerous foveolae in other species).



Figs. 82–84. *S. geminata* group queen alitrunk profiles. 82. *S. saevissima,* with "typical" size, sculpture and pilosity. 83. *S. pythia,* with short, bristle-like pilosity and unusually conspicuous piligerous foveolae. 84. *S. pusillignis,* of uniquely small size and slender build.

NOTES. In the original description of *S. pythia,* Santschi stated that the queens have 10-segmented antennae, rather than the usual 11-segmented antennae of fire ant queens. In fact, the queen described by Santschi does have 10-segmented antennae. Of the 6 other specimens I have studied, one has one antenna 10-segmented

and the other 11-segmented, but the remaining 5 specimens have completely unremarkable 11-segmented antennae.

Unassociated workers like those collected with the distinctive queens of *S. pythia* are distinguishable only with great difficulty from *S. saevissima* (especially the variety *perfida*) occurring in the same area. It has occurred to me that the workers collected with *S. pythia* queens may in fact be depauperate workers of *S. saevissima* from colonies parasitized by *S. pythia,* which in its turn may be without a worker caste. Only further study, perhaps including collections of fresh material for biochemical (especially genetic) analysis will resolve this question.

DISTRIBUTION. The types (examined) are from Loreto, Misiones, Argentina. Other specimens studied are from Botucatu, São Paulo, Brazil. The queen with unequal antennae mentioned above has only the number 189 on the label, but has been retained as part of the Buren collection because of her interesting morphology.

Solenopsis quinquecuspis
Figs. 66, 67, 72, 73

Solenopsis pylades var. *quinquecuspis* Forel 1913:224. Syntype workers. ARGENTINA. Buenos Aires Prov. Bahia Blanca. 28-X-913 (=1913). Zelenko. (MHNB, examined.)
S. geminata saevissima var. *quinquecuspis*: Wheeler 1915:397.
S. saevissima var. *quinquecuspis*: Santschi 1916:381.
S. (*Solenopsis*) *saevissima quinquecuspis*: Creighton 1930:86.
S. blumi Buren 1972:20. Syntype workers. URUGUAY. Colonia Suiza. March 11, 1969. M. S. Blum et al. (WFB, examined.) NEW SYNONYMY.
S. quinquecuspis: Buren 1972:17. In part. (Also in part *S. invicta*.)

MEASUREMENTS AND INDICES: HL 1.10–1.55, HW 0.98–1.55, SL 0.86–1.14, EL 0.18–0.29, PW 0.59–0.98, AL 1.35–2.12, CI 89–101, SI 71–88, OI 15–20. N = 25.

WORKER DIAGNOSIS. Similar to *S. invicta,* but larger; with head broader, (ffv) cordate, with sides convex; posterior border with a concave median impression, this always deeper than in the nearly similar dark southern *S. invicta,* the concavity about 1.1–1.4× as wide as distance between apices of frontal lobes (narrower than in *S. invicta*); mandibles with the usual curvature; mandibular costulae sometimes obsolete mesially, but most often extend entire length of mandible; eye (lv) appears larger than in other species (especially the somewhat similar *S. megergates*), elliptical or ovate, greatest diameter with 11–14 (rarely less) facets, least diameter with 8–10, outer ring of facets rarely depigmented as is common in some species; distance between tip of scape and occipital corner about 0.08–0.15× scape length in major workers, (ffv) in smallest workers scape apex easily reaches or slightly exceeds posterior border; anterolateral pronotal corners (pdv) rounded to weakly angular, tending toward weakly angular in smaller workers, often with anterolateral bosses; propodeal profile with anterior declivity convex, merging into propodeal dorsum by a rounded angle; propodeal dorsum straight, sloping to the rear, descending through rounded angles to declivous face, never forming a continuous convexity with the declivous face; petiolar peduncle shorter than base of node; postpetiolar node in profile lower

than petiole, globular, sometimes with dorsoposterior face a little more convex than anterior face, outline of postpetiolar node (pdv) subrectangular to subtrapezoidal, with dorsal outline nearly flat to weakly concave, and lateral faces straight or concave, subparallel to convergent ventrad; postpetiole 1.07–1.15× as wide as petiole.

Piligerous foveolae of head and thoracic dorsum round, conspicuous, about 0.01 mm or more in diameter (about half or less this in *S. invicta* or, if approaching this size, elliptical in shape, as in darker color variants from southeastern part of range in SE Brazil, Uruguay, Argentina); sculpture otherwise as in *S. invicta* except that of posterior face of petiole and especially postpetiole, which is denser and often extends onto dorsum, especially on transversely rugose-punctate postpetiole.

Pilosity of head and promesonotum abundant, more variable in length than in *S. invicta,* 0.06–0.36 mm; 2–11 erect setae also present on mesopleuron and 1 or 2 on metapleuron, gaster pilosity normal.

Color much less variable than in *S. invicta,* resembling the color of dark *S. invicta*; narrow median frontal impression nearly black, surrounding area dark brown, fading into narrow yellowish surrounding area; clypeus, antennal fossae and sides of head between eye and base of mandible also yellowish; head of less common darker individuals usually concolorous except for dark frontal streak and faintly lighter area near base of mandibles and on clypeus; remainder of head, thorax, propodeum and petiole dark brown, the latter two somewhat lighter ventrally; postpetiole and base of first tergite dusky yellowish to reddish brown; remainder of gaster blackish brown; appendages a little lighter than general color of thorax.

NOTES. The ants that Buren (1972) called *S. quinquecuspis* were mostly the dark southern variant of *S. invicta,* but also included were some true *S. quinquecuspis* which had the characteristic yellowish gaster spot of the first tergite darker than usual. The type series in the Forel collection contains only dark submajors and smaller workers of the latter sort, but Buren did not see these until 2 years after his 1972 publication, rather basing his concept of *S. quinquecuspis* on the description by Creighton (1930). The characters of the mesonotal and propodeal profile presented by Buren for his species *S. blumi* (mesonotum arched, longer than propodeum, the latter with weakly convex dorsal face notably longer than declivous face) are the most common character states in large workers of *S. quinquecuspis,* but they are hardly invariant. Furthermore, the variation in shape of these body parts overlaps broadly the typical shape in *S. invicta,* and this is especially true of workers of less than maximum size. In different individuals of a single colony, the entire range of variation may be expressed. Some samples in Buren's collection bear small pencilled labels in Buren's hand "*blumi* or *quinquecuspis*?," indicating his own (fully understandable) confusion over the distinction between smaller workers of *S. quinquecuspis* and the dark southern *S. invicta.* Metric characters of the largest workers of monogyne colonies may be the only consistent morphological characters for separating in the area where their ranges abut, though genetic and chemical characters seem to provide good separation (Ross and Trager, 1991; Vander Meer, unpubl.).

DISTRIBUTION. The types (examined) of *S. quinquecuspis* came from Bahía Blanca, in southern Buenos Aires province, Argentina. This species occurs from the southern tip of Brazil, south through Uruguay into Argentina including all of Buenos Aires province, most of La Pampa province, and the adjacent fringes of Córdoba and Santa Fé provinces.

Solenopsis richteri

Figs. 52–55

Solenopsis pylades var. *richteri* Forel 1909:267. Syntype workers, queens, male. ARGENTINA. Buenos Aires. Richter. (MHNG, examined.)

S. pylades var. *tricuspis* Forel 1912:397. Syntype workers. ARGENTINA. Buenos Aires Prov. La Plata. BRUCH. (MHNG, examined.)

S. geminata saevissima var. *richteri*: Wheeler 1915:397.

S. saevissima var. *richteri*: Santschi 1916:281.

S. saevissima var. *tricuspis*: Santschi 1916:281.

S. (*Solenopsis*) *saevissima richteri*: Creighton 1930:87; Creighton 1950:232 (In part?).

S. saevissima var. *oblongiceps* Santschi 1936:405. Syntype workers. ARGENTINA. Misiones. Loreto. A. A. Oglobin. (NMB, examined.) NEW SYNONYMY.

S. saevissima richteri: Wilson 1952:66.

S. richteri: Buren 1972:4. Worker, queen, male.

MEASUREMENTS AND INDICES: HL 1.04–1.41, HW 0.87–1.35, SL 0.78–1.13, EL 0.16–0.23, PW 0.55–0.85, AL 1.20–1.84, CI 82–96, SI 77–93, OI 14–17. N = 25.

WORKER DIAGNOSIS. A slender, mostly black species somewhat resembling *S. quinquecuspis* or far southern *S. invicta,* but with the following distinctive features: Head (ffv) elliptical (*oblongiceps*) to weakly cordate in largest workers, with sides convex; posterior border with a concave median impression, the concavity deep and about as wide as distance between apices of frontal lobes; median clypeal tooth often shorter and blunter than in *S. quinquecuspis* or *S. invicta,* and paracarinal teeth often small or absent (*tricuspis*), but this also true in some specimens of other species; clypeal carinae conspicuous, projecting apically as triangular teeth; mandibles with the usual curvature; in large workers mandibular costulae usually obsolete except distally and near base along outer border; eye (lv) ovate, smaller than in *S. quinquecuspis,* often outer ring of facets depigmented, appearing darker than interior facets because of dark background color; anterolateral pronotal corners (pdv) distinctly angular, often with distinct tuberculate or short ridge-like humeral bosses; posterior dorsum usually notably concave mesially (normally convex in all other species); metanotal impression conspicuous; propodeal profile with anterior declivity convex, set off from propodeal dorsum by a rounded angle, occasionally with a ridge at juncture with dorsal face; propodeal dorsum weakly convex, sloping to rear, forming a continuous convexity with the declivous face, or descending through rounded angles to declivous face; petiolar peduncle notably to slightly shorter than base of node; postpetiolar node in profile lower than petiole, globular, sometimes with dorsoposterior face a little more convex than anterior face, outline of postpetiolar node (pdv) nearly globular to subrectangular, with dorsal outline convex, and lateral faces straight, parallel to convergent ventrad; postpetiole 1.04–1.15× as wide as petiole.

Piligerous foveolae of head and thoracic dorsum small, round and inconspicuous, mostly 0.003–0.008 mm in diameter, sculpture otherwise as in *S. invicta,* except postpetiole less sculptured, especially on posterior face, which is transversely rugose on lower third to half, shiny and smooth or faintly tessellate above.

Pilosity as in *S. invicta.*

Color predominantly black with mandibles, lateral lobes of clypeus, antennal fos-

sae, thoracic sutures, tarsi and funiculi, and gaster spot dark brown to yellowish brown; median frontal streak black, but obscured by blackness of surrounding region of many specimens; older preserved material and some fresh specimens paler, with head brown and thorax brown with greater or lesser degree of yellowish mottling.

NOTES. Since I have had the advantage of studying specimens confirmed as hybrids of *S. invicta* and *S. richteri* (through chemical and genetic studies) in order to determine the morphological characteristics of the hybrid, I cannot agree with Buren (1972) that there was little evidence of hybridization among the specimens he studied. In fact, it is clear that much of what he called *S. richteri* was hybrid material, and this from areas along the Gulf Coast from which both *S. richteri* and the hybrid are now completely lacking. It should be noted that specimens of *S. richteri* from some parts of the South American population morphologically resemble hybrids from North America, but other evidence indicates they are not hybrid. "Pure" *S. richteri* from North America is, not surprisingly, less variable morphologically than that from South America.

DISTRIBUTION. The types (examined) were collected in Buenos Aires, Argentina. In the north the limit of the range of *S. richteri* is in southeastern Brazil (Rio Negro, Paraná) and west from there into Misiones province. (Creighton's record from Salta, Argentina, most likely refers to rather dark submajor workers of *S. interrupta,* but I have not seen the specimens he had in mind.) The southern part of the range is delimited by the Atlantic Ocean on the east, and extends west to Mendoza province. In North America, *S. richteri* apparently once occupied much of Alabama and Mississippi, but is now limited to a small portion of northwestern Alabama and northeastern Mississippi. To the south, the current North American range of *S. richteri* is bordered by a broad band of territory occupied by the *S. richteri* × *invicta* hybrid population, encompassing much of northern Alabama and Mississippi and a portion of northwestern Georgia.

Solenopsis saevissima
Figs. 74, 75, 78, 79, 82

Myrmica saevissima F. Smith 1855:166. (Syn-?) type worker. BRAZIL. Para. Rio Tapajós. Bates. (BMNH, examined.)

S. moelleri Forel 1904:174. Syntype workers only. BRAZIL. Santa Catarina. Blumenau. Moeller. (MHNG, examined.) RESTRICTION OF TYPE SERIES. (The male and queen of this taxon are workerless parasites of the *S. daguerrei* group, probably the species known as *S. acuminata*.)

S. moelleri var. *gracilior* Forel 1904:174. Syntype workers. BRAZIL. Ceara. Rocha (leg.). #48. (MHNG, examined.) (Synonymy by Ettershank, 1966:136.)

S. geminata var. *incrassata* Forel 1908:362. Syntype workers. BRAZIL. São Paulo (state). São Paulo. Ihering. (Synonymy by Ettershank, 1966:136.)

S. geminata pylades: Forel 1909:268. NEW SYNONYMY.

(But not *S. geminata pylades* Forel 1904, described from a single queen from Mexico, which is a synonym of *S. xyloni*.)

S. pylades: Forel 1911:279; Forel 1917:723.

S. geminata saevissima: Wheeler 1915:397.
S. geminata saevissima var. *incrassata*: Wheeler 1915:397.
S. saevissima var. *incrassata*: Santschi 1916:380.
S. saevissima var. *pylades*: Santschi 1916:380.
S. saevissima var. *morosa* Santschi 1916:380. Worker. (Synonymy by Ettershank, 1966:136.)
S. geminata saevissima var. *picea* Wasmann 1918:212. Worker, NEW SYNONYMY (*picea* not available in any case, as this name is preoccupied for the small Central American *Solenopsis picea* Emery 1896:89.)
S. saevissima var. *perfida* Santschi 1923:266. Syntype workers. BRAZIL. Minas Gerais. Piracicabo. E. Luja. (NMB, examined.) (Synonymy by Ettershank, 1966: 136.)
S.(*Solenopsis*) *saevissima saevissima*: Creighton 1930:80–83; Wilson 1952:63.
S. saevissima: Santschi 1916:378–380. Buren 1972:15.
S. saevissima var. *picea*: Kistner 1982:73–74 (Table II). NEW SYNONYMY. (See note on *picea,* above.)

MEASUREMENTS AND INDICES: HL 1.00–1.41, HW 0.85–1.38, SL 0.80–1.13, EL 0.16–0.26, PW 0.55–0.88, AL 1.20–1.83, CI 83–96, SI 76–100, OI 14–18. N = 33.

WORKER DIAGNOSIS. A widely distributed, highly variable species which, like *S. geminata,* could easily be separated into morphological species if only peripheral populations were known. More slender, smaller and more strictly tropical than *S. invicta,* and except in color, most closely resembling *S. richteri.* Distinguished as follows: Head (ffv) weakly trapezoidal (slightly broader anteriad) or subquadrate to slightly ovate, with sides straight to weakly convex; posterior border with a concave median impression slightly less to a little wider than distance between apices of frontal lobes; median clypeal tooth poorly-developed, broad-based and blunt, often displaced off center; median clypeal seta conspicuous, arising at or near apex of median tooth; clypeal carinae conspicuous, projecting apically as acuminate, triangular teeth; paracarinal teeth often small or absent, but this also true in some specimens of other species; mandibles with the usual curvature; in large workers mandibular costulae complete or, less often, costulae becoming broader with shallower intercostular furrows on middle, inner portion of upper surface of mandible; eye (lv) ovate, smaller than in *S. quinquecuspis,* often outer ring of facets depigmented; anterolateral pronotal corners (pdv) distinctly angular, but lacking distinct humeral bosses, or these merely small tubercles; posterior pronotal dorsum usually notably flat to weakly convex; promesonotal profile more arched than in *S. richteri*; metanotal impression conspicuous; propodeal profile with anterior declivity convex, set off from propodeal dorsum by a rounded angle, occasionally with a ridge at juncture with dorsal face; propodeal dorsum weakly convex, sloping to rear, forming a continuous convexity with the declivous face, or descending through rounded angles to declivous face; petiolar peduncle notably to slightly shorter than base of node; outline of postpetiolar node (pdv) nearly globular to subrectangular, with dorsal outline convex, and lateral faces straight, parallel to convergent ventrad; postpetiole 1.04–1.15× as wide as petiole.

Piligerous foveolae of head and thoracic dorsum small, round and inconspicuous,

mostly 0.003–0.005 mm in diameter, sculpture otherwise as in *S. invicta,* except postpetiole less sculptured, especially on posterior face, which is transversely rugose on lower third to half, shiny and smooth or faintly tessellate above.

Pilosity as in *S. invicta.*

Color highly variable, the variation partly clinal, with the distribution of color patterns resembling that of *S. invicta,* i.e., predominantly red samples from the north, dark brown samples from the southeast. The following color features may be used in addition to morphology to recognize this species. In western Amazonia (Peru, Rondonia and Acre, Brazil) *S. saevissima* distinguished from sympatric *S. invicta* by lack of median frontal dark streak, and by gaster spot occupying ¾ or more of first tergite. To the south and east, *S. saevissima* specimens are smaller and darker, and most can be distinguished from dark southeastern Brazilian *S. invicta* by the distinctive yellow frons and clypeus (the yellow sometimes extending to include anterior ⅕–⅖ of the head) in high contrast to the brown remainder of head, and by the lack of median frontal dark streak on the more or less bright yellow frons.

NOTES. *S. saevissima* as considered in this study, incorporates a great amount of regional variation. When looking only at the type specimens of forms such as *perfida, incrassata,* and *saevissima,* one is easily convinced they represent separate species. There is, however, abundant additional material available for study which presents a rather confusing panorama of annectant forms and intracolonial variation. From the Brazilian states of Minas Gerais, Goiás and Bahia comes an array of samples including every possible intermediate condition between the typical Amazonian reddish *S. saevissima* and the smaller, darker southern form variously named *incrassata, moelleri,* or *morosa.* While these 2 extremes differ in average size and in color, their proportions and morphology are not particularly distinct. The form *perfida* is apparently more distinctive. The types of this taxon were collected in Minas Gerais. They bear little resemblance to typical *S. saevissima,* and in fact, look more like small, dingy *S. invicta.* I include them in *S. saevissima* because many large samples of the latter from the southern end of its range contain at least a few majors with some or all of the features characteristic of *perfida,* namely broader head with rounded sides, somewhat coarser punctures on the head, and lack of distinctly yellower frons and clypeus relative to the rest of the head.

DISTRIBUTION. The types (examined) of *S. saevissima* were collected along the Tapajós river, in the state of Pará, Brazil. The northern, red form is found virtually throughout Amazonia, and in much of this area is the predominant or only fire ant present, but it does not extend much beyond the limit of the Amazon Shield. A dark variant appears sporadically in Amazonia, but begins to predominate at the southeastern edge of the Amazon drainage in the area from Goiás to Bahia. A tongue of territory occupied by the southern form of *S. saevissima* extends south (the ants coming to smaller average size on the way) through São Paulo to southeastern Brazil.

Solenopsis weyrauchi, new species
Figs. 76, 77, 80, 81

MEASUREMENTS AND INDICES: HL 1.02–1.34, HW 0.85–1.18, SL 0.78–1.02, EL 0.14–0.19, PW 0.57–0.75, AL 1.18–1.67, CI 85–92, SI 83–94, OI 13–15. N = 12.

HOLOTYPE MEASUREMENTS: HL 1.34, HW 1.18, SL 0.98, EL 0.19, PW 0.74, AL 1.67, CI 88, SI 83, OI 14.

WORKER DIAGNOSIS. Ecologically unusual within this subcomplex, this species is superficially unremarkable, resembling a slender *S. saevissima,* but distinguished as follows: Head (ffv) elongate, subrectangular, sides straighter than typical for *S. saevissima*; posterior border with a concave median impression somewhat narrower than distance between apices of frontal lobes; median clypeal tooth even more poorly-developed than in *S. saevissima,* most often lacking altogether; median clypeal seta conspicuous, arising near apex of median tooth or in middle or clypeal margin, sometimes off-center; clypeal carinae weakly developed, cross section through middle of clypeus a flattened trapezoid without ridges at angles between upper and declivous faces; clypeal carinae developed apically, at margin forming usually very short, acuminate teeth; paracarinal teeth small or absent; mandibles with the usual curvature; in workers of all sizes, mandibular costulae 5–6 (usually 7 or more in other species), costulae becoming broader with shallower intercostular furrows on middle and on upper surface of mandible, obsolescent near base; eye (lv) ovate, smaller than in *S. saevissima,* greatest diameter with 10–11 facets, least diameter with 7–8, often outer ring of facets depigmented; anterolateral pronotal corners (pdv) rounded, never angular, but may bear minute humeral small tubercles; convex; pronotal profile convex, blending insensible into flatter mesonotal profile; metanotal impression, propodeal profile, and conformation of petiole and postpetiole not appreciably different from those of *S. saevissima.*

Piligerous foveolae of head and thoracic dorsum round, more conspicuous than in *S. saevissima,* mostly 0.005–0.01 mm in diameter, sculpture otherwise as in *S. invicta,* postpetiole more sculptured than *S. saevissima,* especially on posterior face, which is transversely rugose on lower ½–¾, generally smooth with conspicuous piligerous foveolae above.

Pilosity a little more abundant than in *S. saevissima,* mesonotum of large workers with about 30 erect setae, (20–25 in *S. saevissima*).

Color striking, head (at least anterior portion), mesonotum and gaster spot (when present) bright reddish yellow; remainder of gaster blackish brown; propodeum, dorsum of petiole and postpetiole, and sometimes rear portion of head, pronotum and region of frons surrounding median streak yellowish brown with brown spots set off by rather distinct borders from surrounding lighter areas; median frontal streak small, blackish, often formed of 2 elongate dots; gaster spot marked with 2 small anterolateral spots in lighter specimens, or may be reduced to a mere anterior yellowing in darker specimens, which lack a distinct tergal spot.

NOTES. All but one pin of the known specimens of *S. weyrauchi* were collected by the German collector Weyrauch in the early part of this century, hence the name. Weyrauch's specimens were ultimately deposited at the Instituto Miguel Lillo in Tucumán, Argentina, and a few ended up in the USNM and MZSP. It is possible he took duplicate material back to Germany, but I have been unable to locate it.

The queen of this species is not morphologically distinguishable from those of most other *saevissima* subcomplex species, especially *S. invicta* and *S. saevissima. S. weyrauchi* queens do, however, share the striking bright yellow ground color and dark brown markings of the worker, including, in all 3 specimens observed, the 2 anterolateral dark spots within the yellow gaster spot on the first tergite.

This species is unusual in that it is apparently restricted to the high altitude grasslands of the Peruvian Andes. According to altitude data on the collection labels, the specimens were collected at altitudes from a moderately surprising 2,500 m to a barely credible 4,300 m.

DISTRIBUTION. The types are labelled "Abra Gavilán b. Cajamarca, 2,800 m. PERU. #709. ex. col. Weyrauch." *S. weyrauchi* is known from only a few widely separated localities in the Peruvian Andes. Further collecting may well reveal its occurrence in Andean localities from Colombia to Argentina and Chile.

TYPE DEPOSITION. The holotype is the largest of 6 workers mounted on 3 points on a single pin to be deposited at LACM. The remaining 23 paratypes (same collection data) and the other specimens borrowed from IML will be returned there, except for 2 pins bearing a total of 9 specimens which will be sent to LACM and MCZ.

ELECTRA SUBCOMPLEX

Solenopsis electra, **New Status**

Figs. 38, 39, 42, 43

Solenopsis pylades electra Forel 1914:397. Syntype workers. ARGENTINA. Salta. Jujuy. XI-913 (=1913). Schuer. #129. (MHNG, examined.)
S. (*Solenopsis*) *saevissima electra*: Creighton 1930:92. Worker, queen.
S. saevissima electra: Santschi 1916:381.
S. saevissima saevissima cline *S. saevissima richteri* (Bolivia variant) Wilson 1952: 65. (Specimens identified by Wilson in MCZ examined.) NEW SYNONYMY.
S. saevissima saevissima cline *S. saevissima richteri* subsp. *electra* Wilson 1952:65. (Specimens identified by Wilson in MCZ examined.)

MEASUREMENTS AND INDICES: HL 1.05–1.35 (1.40–1.55), HW 0.90–1.23 (1.33–1.48), SL 0.90–1.00 (1.08–1.13), EL 0.19–0.24 (0.25–0.26), PW 0.55–0.68 (0.75–0.85), AL 1.28–1.53 (1.70–1.98), CI 86–95 (91–99), SI 74–100, OI 16–19. N = 23. Values in ( ) are for robust specimens from large colonies from the vicinity of Cochabamba, Bolivia.

WORKER DIAGNOSIS. Head (ffv) subovate, with sides convex; posterior border with a concave median impression, concavity shallow and about 1–1.5 × or more as wide as distance between apices of frontal lobes; median clypeal tooth well-developed, usually sharp, 0.5–1 × as long as lateral teeth, sometimes displaced off center; on some specimens, a smaller second, off-center intercarinal tooth occurs, rarely this and median tooth nearly equal in size; median clypeal seta conspicuous, arising at or near apex of median tooth; clypeal carinae conspicuous, projecting apically as acuminate, triangular teeth, or curved mesad and faintly falcate; space between clypeal carinae concave, except near base of median tooth (teeth); mandibles with the usual curvature; mandibular costulae mostly complete, broader and flatter in inner, mesial portion of upper mandibular surface; eye (lv) ovate, greatest diameter with 11–13 (rarely less) facets, least diameter with 8–9, often outer ring of facets depigmented, especially anteriorly; anterolateral pronotal corners (pdv) rounded, lacking protruding angles; this species unique in that in workers of all sizes, pronotal profile a continuous nearly flat to weakly convex surface, rarely with even the least hint of more vertical anterior declivity and more horizontally oriented dorsal surface as found in all other

fire ants; anteroventral border of mesopleuron with a seam-like flange and often a lobate anteroventral projection on lower ⅓–½, (unlike projection of *S. geminata,* which is most often placed near middle of mesopleural border; propodeal profile with anterior declivity convex, set off from propodeal dorsum by a rounded angle; propodeal dorsum flat or weakly convex, descending through rounded angles to declivous face, or rarely forming a continuous convexity with the declivous face, latter 2 faces at approximately a right angle; petiolar peduncle slightly shorter than base of node; postpetiolar node in profile lower than petiole, globular; outline of postpetiolar node (pdv) subglobular, with dorsal outline convex, and lateral faces straight, parallel to convergent ventrad; postpetiole 1.04–1.15× as wide as petiole.

Piligerous foveolae of head and thoracic dorsum typically small, round and inconspicuous, mostly 0.003–0.005 mm in diameter; sculpture of mesometapleuron (lv) consisting of fine longitudinal rugose striae, often with interstitial punctation or areolation, striation obsolete above leaving only faint punctation; dorsum of propodeum unsculptured; area surrounding propodeal spiracle unsculptured anterodorsally, but behind spiracle, weak irregular punctation often partially obscures sheen of circumspiracular area (though less so than in *S. pusillignis,* where this area is heavily punctate and dull); declivous face of propodeum with transverse striae contiguous with those of metapleuron; petiolar peduncle, and sometimes base of node, weakly areolate; venter of petiole with longitudinal median carina and ventral process obsolete, consisting of a small truncate projection; petiolar node largely unsculptured except piligerous foveolae, and perhaps a few shallow longitudinal furrows; dorsum of postpetiole unsculptured other than piligerous foveolae; posterior face of postpetiole mostly shiny near top, transversely rugose-striate on lower ⅔, with interspersed punctation below.

Pilosity of head and promesonotum moderately abundant to abundant, like that of *S. invicta.*

Color variable, though generally fairly consistent within a colony; most often bicolored with head (except posterior border and a triangular area the apex of which is at the position of the median ocellus, the latter rarely present), legs, and antennae reddish yellow; mandibles brown; thorax and gaster darker brown with yellowish areas near sutures and anterior portion of first tergite; less often darker, ranging from dark brown with anterior portion of head, scapes and legs dingy yellow, to uniform brownish black with only frons and legs slightly lighter. The darker forms are more common in Bolivia, the lighter ones to the south.

NOTES. Since *S. electra* is normally bicolored and lives in poorly marked nests in well-drained soil, this species is somewhat reminiscent of a polymorphic *S. substituta.* It has been collected in desert and chaco areas in the lowlands, and occurs in rocky, exposed sites in the Andean foothills.

In the Bolivian part of its range this species is considerably more robust than in Argentina and Paraguay (see measurements and indices). If we knew this ant only from the south, it would be safe to characterize it as a small fire ant, but the major workers of the large northern variant of *S. electra* fall well within the size range of, say, *S. interrupta,* a mid- to large-sized fire ant. As in the related species *S. pusillignis* (see discussion of that species), even where it develops the larger major workers *S. electra* has its characteristic small queens and males.

DISTRIBUTION. *S. electra* was described from Salta, Jujuy, Argentina, approx-

imately in the middle of its range. Specimens I have seen come from Cochabamba and Santa Cruz, Bolivia south to Santiago del Estero province, Argentina. Creighton lists a credible locality in Córdoba, while a sample I examined from Asunción, Paraguay seems to be far east of the normal range, may represent an introduction from the west.

Solenopsis pusillignis, new species
Figs. 40, 41, 44, 45, 84

MEASUREMENTS AND INDICES: HL 1.03–1.33 (1.50–1.60), HW 0.88–1.24 (1.43–1.54), SL 0.80–0.98 (1.00–1.05), EL 0.21–0.26 (0.28–0.29), PW 0.53–0.69 (0.78–0.83), AL 1.20–1.55 (1.63–1.80), CI 85–94 (95–98), SI 77–91 (68–70), OI 18–22. N = 21. Values in ( ) are for 5 large, robust specimens from 2 colonies from the vicinity of Corumbá, Mato Grosso do Sul, Brazil. See discussion.

HOLOTYPE MEASUREMENTS: HL 1.25, HW 1.18, SL 0.98, EL 0.25, PW 0.63, AL 1.45, CI 94, SI 83, OI 20.

WORKER DIAGNOSIS. The smallest fire ant, superficially resembling North American *S. aurea,* but differing as follows: Head (ffv) subovate with shallow median posterior concavity as in *S. electra,* the concavity usually about as wide as distance between apices of frontal lobes; median clypeal tooth always present, usually sharp and 0.5× (or a little less) as long as lateral teeth, rarely displaced off center; median clypeal seta conspicuous, arising at or near apex of median tooth; clypeal carinae conspicuous, projecting apically as triangular teeth; space between clypeal carinae concave, except near base of median tooth; mandibles with the usual curvature; mandibular costulae complete, configured as in *S. electra*; remainder of head structurally as in *S. electra*; anterolateral pronotal corners (pdv) rounded-angular, with faint ridge-like humeral bosses; propodeal profile like that of *S. electra,* but with dorsal face more often sloping posteriad; remainder of body like a small *S. electra,* except petiolar and postpetiolar node profiles a little thicker.

Piligerous foveolae of head and thoracic dorsum typically small, a little more conspicuous than in *S. electra,* mostly 0.005–0.008 mm in diameter, but occasionally up to 0.01 mm; sculpture of mesometapleuron (lv) unusually well developed, especially for a fire ant of this small size, consisting of fine longitudinal striae or rugose striae, interstitial punctation strongly developed and extending beyond limits of striation dorsad; punctation nearly surrounding and contiguous with propodeal sculpture except for a small shiny area anterior to spiracle; declivous face of propodeum with transverse striae contiguous with those of metapleuron, and with well developed interstrial punctation; petiolar peduncle, and sometimes base of node, weakly areolate; remainder of sculpture as in *S. electra.*

Pilosity as in *S. electra,* of the *S. invicta* type.

Color like that of *S. aurea,* light brownish yellow with brown extremities, to more uniform yellowish brown.

NOTES. The name *pusillignis,* referring to the small size and relatively mild sting, means "little fire."

S. pusillignis is known only from the 2 localities mentioned below. Colonies from Corumbá produce workers significantly larger than those in the Cuiabá area, but the sexuals are about the same size. These queens are the smallest of any cis-Andean

fire ant, about the same size as those of *S. gayi,* or of the non-fire ant, *S. wasmanni. S. pusillignis* seems truly to be a "cerrado ant," the only fire ant that lives in relatively undisturbed cerrado. It may also be found in disturbed cerrado, but is often displaced by *S. invicta* (or *Paratrechina fulva* in some areas) in cerrados subject to heavy grazing. The preferred habitat seems to be at or near the edges of grassy temporary ponds (campo limpo), but it is also found in better drained sites.

DISTRIBUTION. The types were collected in a cerrado remnant (now largely destroyed) on the Federal University campus in Cuiabá, Mato Grosso, Brazil. *S. pusillignis* is so far known only from the vicinity of Cuiabá, Mato Grosso and Corumbá, Mato Grosso do Sul, Brazil.

TYPE DEPOSITION. The holotype worker and 5 paratypes (including 2 queens) will be placed in MZSP. Fifteen remaining paratypes and numerous other specimens will be divided between AMNH, BMNH, FSCA, LACM, MCZ and MZSP.

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NEW NEARCTIC CHLOROPERLIDAE (PLECOPTERA)

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Abstract.—Two new species of Nearctic Chloroperlidae are described: *Sweltsa voshelli* from Virginia and *Suwallia wardi* from Colorado. A key is provided for the identification of adult males of the eastern Nearctic species of *Sweltsa.*

There are presently 22 Nearctic *Sweltsa* species, of which six are eastern in distribution (Kirchner and Kondratieff, 1988; Stark et al., 1986; Surdick, 1985). A seventh species has been known from the Blue Ridge Mountains of southwestern Virginia for some time, and is described below.

Sweltsa voshelli Kondratieff and Kirchner, new species

Male.—Body length 7.0–7.5 mm; length of forewing 8.5–9.0 mm. General color bright yellow in life (yellow-white in alcohol). Pronotum with black margin, no center stripe. Middorsal region of abdominal terga 1–9 with black dash or mark. Terga 9 with transverse ridge (Figs. 1–2). Epiproct erectile, elongate, inflated, forming a flange dorsally (Fig. 1), in lateral view tapering evenly to a hook (Figs. 2–3).

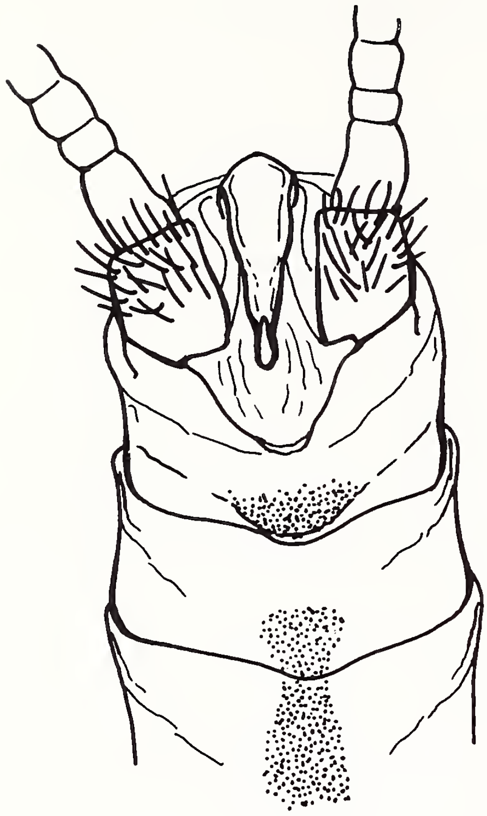
Female.—Body length 8.0–9.0 mm; length of forewing 9.0–10.0. General habitus and coloration similar to male. Subgenital plate rounded, extending to 8th sternum.

Types.—Holotype male, allotype female, Patrick Co., Virginia, small spring-fed stream bordering cemetery, Co. Rt. 605, 10 May 1982, B. C. Kondratieff; paratypes: same data as holotype 23 males, 10 females; same data except 10 May 1983, 10 males, 6 females; same data except 24 May 1990, B. C. Kondratieff, R. F. Kirchner and J. L. Welch, 7 males and 26 females; Patrick Co., Big Cherry Creek, Co. Rt. 637, 27 May 1983, B. C. Kondratieff, 1 male.

The holotype and 3 paratypes will be deposited in the collection of the United States Museum of Natural History, the remaining paratypes in the Kirchner Collection, Colorado State University Insect Collection, Virginia Tech, and Monte L. Bean Life Science Museum, Brigham Young University.

Etymology.—This species is named in honor of Dr. J. Reese Voshell, Jr., Virginia Polytechnic Institute and State University for his many contributions to knowledge of the aquatic insects of Virginia. He also helped stimulate the senior author's interest in aquatic biology.

Diagnosis.—*Sweltsa voshelli* belongs to a group of species which include *S. mediana*



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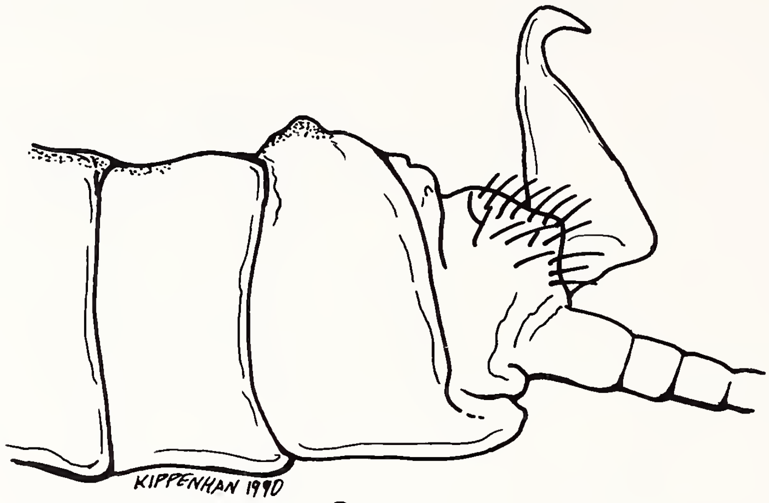

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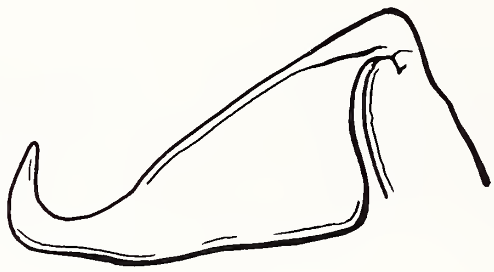

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Figs. 1–3. *Sweltsa voshelli.* 1. male terminalia, dorsal view. 2. male terminalia, lateral view. 3. epiproct, lateral view.

(Banks), *S. onkos* (Ricker), *S. pocahontas* Kirchner and Kondratieff, and *S. urticae* (Ricker). The male is most similar to *S. urticae,* but it can be easily distinguished by the even tapering of the epiproct to its hook (in lateral view) (Figs. 2–3), whereas, the epiproct of *S. urticae* abruptly narrows basally and has a U-shaped, notched hook (Fig. 7).

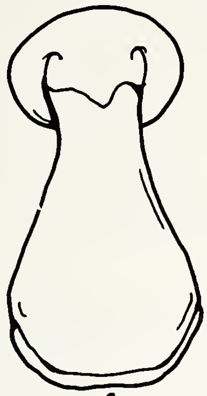
The female of *S. voshelli* can be usually distinguished from all other eastern species by the combination of the prothorax lacking a brown or black center stripe and the rounded subgenital plate. However, the subgenital plate is similar to *S. pocahontas* and *S. urticae.*

Other stoneflies collected with *S. voshelli* were *S. lateralis* (Banks), *Alloperla usa* Ricker, *Peltoperla tarteri* Stark and Kondratieff, *Ostrocerca truncata* (Claassen), *Amphinemura nigritta* (Provancher), and *Isoperla* sp.

The following key will separate males of the seven eastern species of *Sweltsa.*

KEY TO THE MALES OF EASTERN NEARCTIC SPECIES OF *SWELTSA*

1\. Epiproct spatulate, flattened dorsoventrally (Fig. 4); head with dark pattern .... *S. naica* (Provancher)
– Epiproct laterally compressed or inflated, terminating in a hook process (Figs. 2, 3, 5–9); head pale, at most with dark ocellar rings 2
2\. Prothorax margined with dark brown or black 3
– Prothorax not margined brown or black 6



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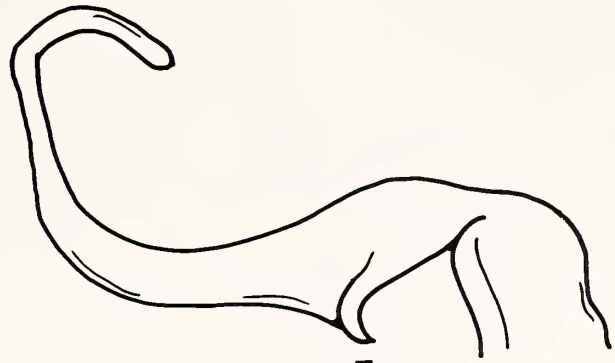

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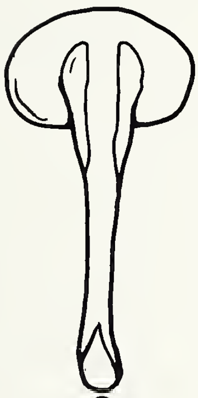

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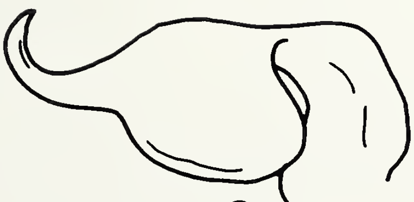

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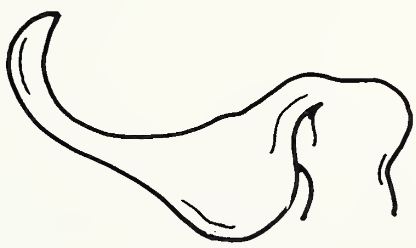

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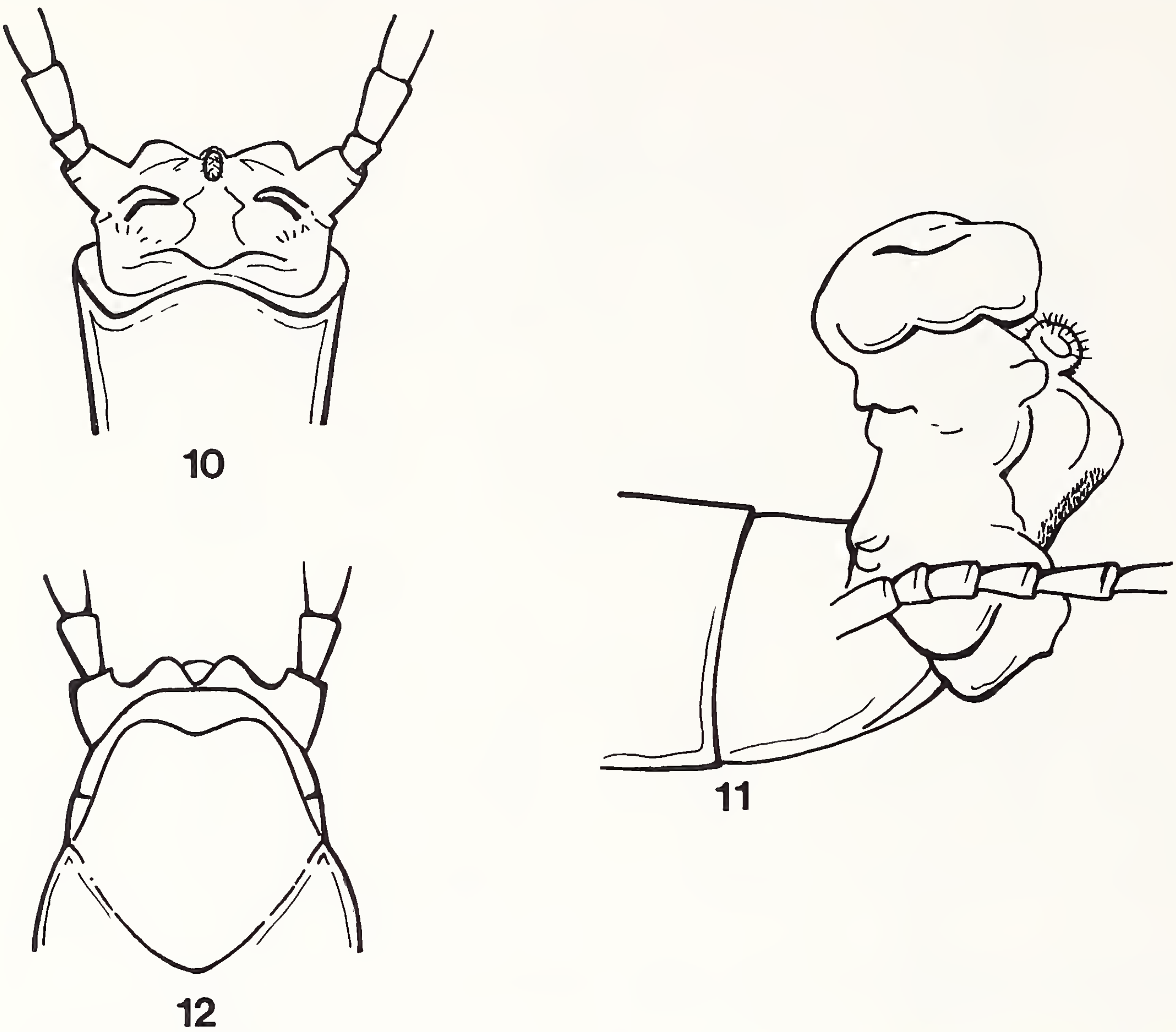
Figs. 4–9. 4. *Sweltsa naica,* epiproct dorsal. 5. *Sweltsa lateralis,* epiproct lateral. 6. *Sweltsa pocahontas,* epiproct dorsal. 7. *Sweltsa urticae,* epiproct lateral. 8. *Sweltsa mediana,* epiproct lateral. 9. *Sweltsa onkos,* epiproct lateral.

3. Epiproct in lateral view, long, slender, with hook recurved (Fig. 5) . . . *S. lateralis* (Banks)
– Epiproct in lateral view, short, expanded basally; hook not recurved (Figs. 2, 3, 6–9) 4
4. In dorsal view, epiproct inflated basally, flanged dorsally before hook (Fig. 1) 5
– In dorsal view, epiproct not inflated basally, subparallel before hook (Fig. 6) . . . .
. . . . *S. pocahontas* Kirchner and Kondratieff
5. In lateral view, epiproct evenly tapering to hook (Fig. 1) . . . .
. . . . *S. voshelli* Kondratieff and Kirchner



Figs. 10–12. *Suwallia wardi.* 10. male terminalia, dorsal view. 11. male terminalia, lateral view, aedeagus extruded. 12. female terminalia, ventral view.

– In lateral view, epiproct with a deep U-shaped notched hook (Fig. 7) ..... *S. urticae* (Ricker)
6. In lateral view, epiproct with neck of hook short, basal lobe abruptly expanded (Fig. 8) .... *S. mediana* (Banks)
– In lateral view, epiproct, with neck of hook long, tapered to basal lobe (Fig. 9) .... *S. onkos* (Ricker)

The genus *Suwallia* presently includes 5 Nearctic species, with 4 of these restricted to the western states (Surdick, 1985). A large and distinctive undescribed species was collected from a short stretch of snow-melt run entering a small pond at 2,460 m. This locality is located in the foothills of the eastern side of the Front Range of the Rocky Mountains of Colorado. This area is typified by sparse stands of ponderosa pine and small patches of quaking aspen in wetter soils. This species was not collected from nearby Elkhorn Creek and its small tributaries, however two chloroperlids, *Triznaka pintada* (Ricker) and *Sweltsa lamba* (Needham and Claassen) were abundant in these streams. No other Plecoptera were collected in association with the new species.

Suwallia wardi Kondratieff and Kirchner, new species

Male.—Body length 9.5–10.5 mm; length of forewings 9.0–9.5 mm. In life, head lemon yellow, prothorax bright pea green, abdomen green (yellow-white in alcohol).

Middorsal black marks on abdomen often faint, reduced or absent, if present on abdominal terga 1–5 or 1–6. Hemiterga 10 with medially directed narrow digitate process. Epiproct typical, weakly erectile, bulb-like and setose (Fig. 10). Aedeagus with a large expanded apical lobe, two rounded lateral lobes, and a large broad anteriorly directed lobe (Fig. 11); with a patch of two parallel bands of setae basally.

Female.—Body length 11.0–11.5 mm; forewing length 11.0–12.0 mm. General coloration similar to male; middorsal abdominal black marks or dashes terga 1–6 or 7; subgenital plate broadly truncate and emarginate apically (Fig. 12).

Types.—Holotype male and allotype female, Larimer Co., Colorado, small stream entering upper pond, Ben Delatour Scout Ranch, 21 June 1990, B. C. Kondratieff. Paratypes: 23 males and 19 females, same data as holotype.

The holotype and 3 paratypes will be deposited in the collection of the United States Museum of Natural History, the remaining paratypes in the Kirchner Collection, Colorado State University Insect Collection, and Monte L. Bean Life Science Museum, Brigham Young University.

Etymology.—The patronym honors Dr. James V. Ward, Colorado State University for his substantial contributions to aquatic ecology. Dr. Ward has also added much to the knowledge of the aquatic insects of Colorado.

Diagnosis.—Both sexes of *S. wardi* can be immediately distinguished from all other described Nearctic species, especially from the very closely related *S. pallidula* (Banks) and *S. lineosa* (Banks) by its "*Alloperla*"-like color (in life: lemon yellow head, pea green prothorax, pea green abdomen), lacking dark pronotal margins, and reduced and sometimes absent median longitudinal abdominal stripe. Both *S. pallidula* and *S. lineosa* are yellow to light fuscous in life with dark pronotal margins and usually with well-developed median abdominal stripes. Additionally, the male of *S. wardi* can be distinguished from both species by the form of the aedeagus (Fig. 11), especially the large expanded apical lobe, and the parallel band of setae basally. The large broad female subgenital plate of *S. wardi* is similar to that of *S. lineosa* but tapers more apically.

ACKNOWLEDGMENTS

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A REVIEW OF THE VELIID FAUNA OF BROMELIADS, WITH A KEY AND DESCRIPTION OF A NEW SPECIES (HETEROPTERA: VELIIDAE)

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Abstract.—Bromeliad inhabiting Veliidae are restricted to the New World tropics, and no exploitation of similar phytotelmata habitats is known among veliids in any other tropical region. The eight species of bromeliadicolus Veliidae occurring in the Neotropical region are discussed, and a key to the species provided. A new species, *Paravelia paolettii* is described from Venezuela.

Among the more interesting ecological segregates within the Neotropical Veliidae is the guild of species restricted to the water pockets of terrestrial and arboreal bromeliads. Including the new species proposed herein, eight species of Veliidae are now known which are apparently restricted to this unusual microhabitat. Of these, four species belong to the genus *Microvelia* Westwood and four species to the genus *Paravelia* Breddin. To date these are the only genera of surface dwelling Heteroptera recorded from this habitat, although members of the subaquatic family Corixidae are also found there on rare occasions. Outside of the original species descriptions mentioning the bromeliad habitat, no review of these interesting insects has appeared except for a brief discussion in Drake and Hussey (1954).

All Veliidae so far known from container habitats are restricted to the New World; these habitats include bromeliads (treated in greater detail below), crab holes (with two apparently obligate species of *Microvelia, M. oraria* Drake and *M. inquilina* Polhemus and Hogue, both from Costa Rica; see Polhemus and Hogue, 1972 for discussion), and tree holes (*Paravelia mysersi* Hungerford from Trinidad; see Hungerford, 1931). *Microvelia atrata* Bueno from the southeastern United States occurs in the dark recesses of hollowed out cypress tree boles and so might also be included in this ecological assemblage.

The veliid species that we have collected in bromeliads are usually found between the rather tightly fitting leaves in the center of the plant which trap rainwater in a series of deep pockets, and never occur in bromeliads that lack such water pockets. Among the taxa involved, the *Paravelia* species appear to prefer ground dwelling bromeliad species, while the *Microvelia* species have been taken from both terrestrial and arboreal bromeliads. *Paravelia* and *Microvelia* are in different subfamilies (Veliinae and Microveliinae respectively), so it is clear that adaptation to the bromeliad habitat has occurred on at least two separate occasions. Even so, there are convergent similarities in appearance among all bromeliadicolous species. The macropterous forms possess bright yellow or white spots on the hemelytra, and in the genus *Paravelia*

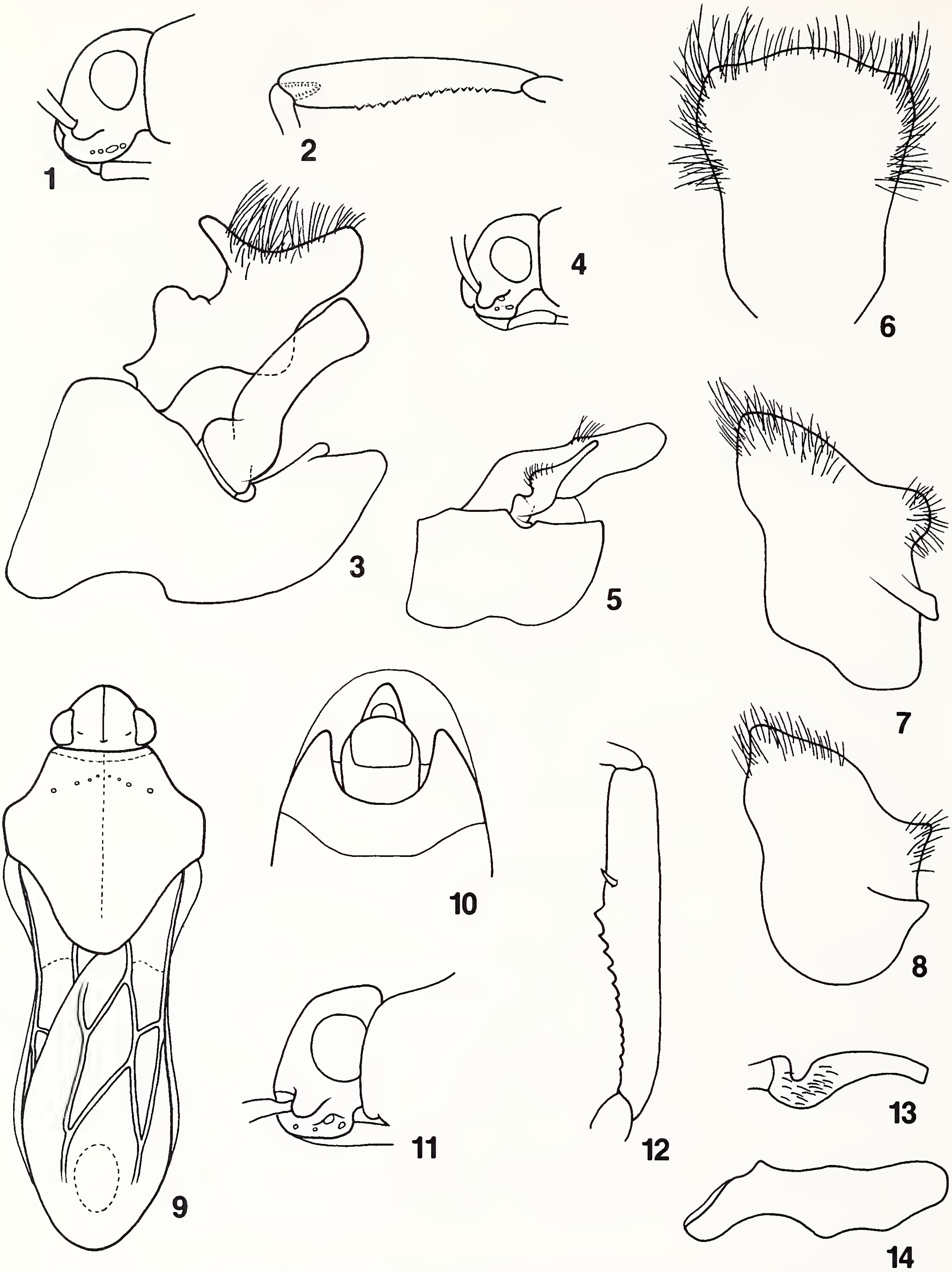
only this morph is known. In *Microvelia* every known bromeliad inhabiting species has in addition either a micropterous or an apterous morph with light markings dorsally in the same position as the light wing spots of the winged morph; in *M. laesslei* these are white micropterous wing pads, in *M. distanti* they are a combination of light colored regions of the integument and silvery pubescent areas, and in *M. ancona* and *M. oaxacana* they are simply bright silvery pubescent areas.

We have found that bromeliadicolous veliids are generally not evenly distributed within a patch of bromeliads, but instead tend to aggregate in certain individual plants. While most bromeliads searched will contain only one or two insects, or more commonly none at all, occasional plants are found which contain up to a dozen. In such preferred plants it is often possible to see one or more specimens in a water pocket using a flashlight, and once located they can sometimes be seen even in ambient light, moving about as ghost-like creatures on the water surface, with only the bright markings visible. The ground dwelling bromeliads that harbor these veliids are often rather large plants which may occur either on the forest floor or on sheer cliffs where collecting is distinctly hazardous. In many instances the plant must be cut off near the base and the leaves peeled away one at a time while each is searched for the veliids, which once exposed run rapidly over the leaf surfaces and attempt to hide in crevices, or move to the dark undersides of the remaining leaves. The most effective way to collect them under such circumstances is by use of an aspirator, with one person dismembering the bromeliad while a second stands ready to suck up the escaping insects.

Most of the specimens upon which this study was based are held in the J. T. Polhemus collection, Englewood, Colorado (JTPC). Abbreviations for depositories of other specimens examined are given in the acknowledgments. All measurements are given in millimeters.

KEY TO THE SPECIES OF BROMELIAD INHABITING VELIIDAE

1. Length greater than 3.2 mm. Tarsal formula 3:3:3 .... *Paravelia* 2
1′. Length less than 2.5 mm. Tarsal formula 1:2:2 .... *Microvelia* 5
2. At least head bright orange-red. Male hind tarsi not fusiform 3
2′. No part of head or body bright orange-red. Male hind tarsi fusiform 4
3. Head and body bright orange-red; hemelytra black with white spots .... *helenae*
3′. Head only bright orange-red; hemelytra black with yellow spots .... *paolettii*
4. Body markings brownish; hemelytra brownish with white spots; distal hemelytral spot ovate or round, not approaching apex; pronotum anteriorly occasionally orange brown, sometimes with silvery frosting, but never marked with bright yellow .... *recens*
4′. Body markings black; hemelytra black with yellow spots; distal hemelytral spot elongate, reaching apex or nearly so; pronotum anteriorly with bright yellow transverse markings .... *manausana*
5. Ground color brownish 6
5′. Ground color black or blackish gray 7
6. Apterous form brownish with bluish silvery spots on abdominal dorsum; micropterous form unknown; in macropterous form, hemelyra brown with 6 to 8 white elongate spots .... *oaxacana*
6′. Apterous form unknown; micropterous form with oval white wing pads; in macropterous form, hemelyra brown with entire basal ⅓ white .... *laesslei*
7. Connexiva entirely dark .... *ancona*



Figs. 1–14. 1–3. *Paravelia manausana* J. & D. Polhemus. 1. Head, lateral view. 2. Posterior femur, posterior view. 3. Male genitalia, lateral view. Cl = clasper or paramere; Pg = pygophore; Pr = proctiger. 4–8. *Paravelia recens* Drake & Harris. 4. Head, lateral view. 5. Male genitalia, lateral view (Brazil). 6. Male first genital segment, dorsal view (Brazil). 7. Male first genital segment, lateral view (Brazil). 8. Male genitalia, lateral view (Bolivia). 9–14. *Paravelia paolettii* new species. 9. Habitus. 10. Male abdominal terminalia, ventral view. 11. Head, lateral view. 12. Posterior femur, posterior view. 13. Male clasper or paramere. 14. Male proctiger.

7′. First three connexival segments white or yellow in both apterous and macropterous forms .... *distanti*

Paravelia helenae (Hungerford)
Fig. 19

Velia helenae Hungerford 1929. Holotype, female, Peru, Callanga [Dept. Cuzco, 1,500 m], Riksmuseet, Stockholm.
Velia helenae, Polhemus 1969. Description of male; distribution record, Dept. Junin, Peru.
Paravelia helenae, Polhemus 1976:512. New combination.

Discussion. This species was sought for many years by professional collector Felix Woytkowski (1974) at the request of H. B. Hungerford, who had described it from a single female he found in the Stockholm museum. Unfortunately it was not known that the species was an obligate bromeliad inhabitant, so Woytkowski undoubtedly passed close by many populations on his way to search for it diligently in the "normal" aquatic veliid habitats. This elusive species was finally rediscovered in 1965 by Pedro Wygodzinsky, who noted that his specimens came from bromeliads on a cliff.

Material examined. PERU: Dept. Junin: 5 males, 7 females, 1 nymph, Huacapistana, 1,800 m, 30 July 1965, B. & P. Wygodzinsky (AMNH, JTPC).

Paravelia manausana J. & D. Polhemus
Figs. 1–3, 18, 19

Paravelia manausana J. T. Polhemus & D. A. Polhemus 1984:341. Holotype, male, Brazil, Manaus, Zoologische Sammlung des Bayerischen Staates (ZSMC), Munich.

Discussion. This species is most closely related to *Paravelia recens* (Drake & Harris) but may be separated by the characters given in the key and larger size.

When we originally described *P. manausana* we hypothesized that it inhabited bromeliads based on its similarity to *P. recens,* even though we lacked supporting habitat data. This hypothesis was confirmed when we collected the species from water filled leaf axils of terrestrial bromeliads at Reserva Ducke, northeast of Manaus, Brazil. The area in which the species occurred was a "campina" forest growing on poor, sandy soil. Two types of terrestrial bromeliads were present in the understory, a larger one with stiff, spiny-edged leaves and pink flowers, and a slightly smaller one with flexible, smooth edged leaves and no flowers. The veliids were found only in the latter type of bromeliad; a comparison with INPA herbarium specimens indicated that the species in question was probably *Vriesia splitgerberi* Ruby Branga 1975, which occurs on sandy soils from Manaus north to Roraima. Only three specimens of *P. manausana* were taken, all from the same plant. By contrast, *P. recens* was common, occurring in nearly every water-bearing plant examined.

We also collected *P. manausana* in Bolivia from large terrestrial bromeliads growing on cliffs in the Rio Coroico gorge above Caranavi. These bromeliads were restricted to very sheer rock faces, and required ropes to reach. As at the Reserva Ducke locality, there were two types of terrestrial bromeliads at this site, a stiff spiny one and a flexible, smooth-leaved one, with the veliids occurring only in the latter. It appears that this preference for the smooth-leaved bromeliads is due in part to

their superior water holding ability, even though their lack of spines offers less protection from potential predators. Once again *Paravelia recens* occurred sympatrically in the same plants at this locality.

The male pygophore of *P. manausana* is distinctively sculptured (Fig. 3), but differs somewhat between the two series mentioned above. We originally thought the Bolivian population represented a new species, but have concluded that the variability does not warrant the proposal of a new taxon, became most important characteristics are very similar, and there is also variation within any given population.

In our original paper (Polhemus and Polhemus, 1984) specimens of *P. recens* were included in the type series of *P. manausana* by error. These are relisted in the present work in the material examined section under *P. recens*.

In addition to the Brazilian host plant record, a single specimen is also at hand from Ecuador which was intercepted by U.S. Customs at the Miami airport on a bromeliad belonging to the genus *Guzmania*.

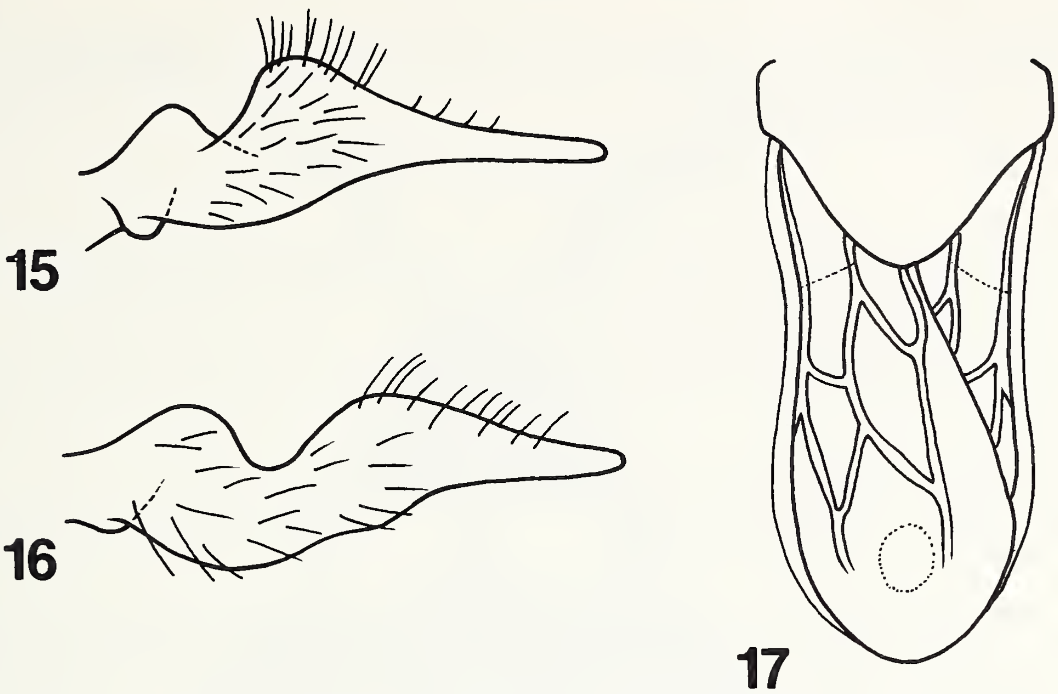
Material examined. BOLIVIA: Dept. La Paz: many males and females, Rio Coroico gorge, 28 km W Caranavi, bromeliads on cliffs, Cl 2523, 15 November 1989, J. T. & D. A. Polhemus (IELB, JTPC). BRAZIL: Amazonas: Type-series, 3 males, 3 females, Manaus, Rio Branco, 4 December 1969, E. J. Fittkau (ZSMC, JTPC); 2 males, 1 female, nr. Manaus, Reserva Ducke, Ig. Acará, bromeliads [*Vriesia splitgerberi* ?] on forest floor, Cl 2476, 26 August 1989, J. T. & D. A. Polhemus (INPA, JTPC). ECUADOR: 1 female, on *Guzmania* sp., intercepted at Miami, 2 June 1988, W. C. James (USNM). PERU: Dept. Pasco: 1 female, Pan de Azucar, 13 July 1961, F. S. Truxal (LACM). VENEZUELA: T. F. Amazonas: 3 males, 5 females, 5 immatures, Cerro Unturan Camp, 65°14′W, 01°33′N, 1,100 m, 11–15 February 1989, from large terrestrial bromeliad, Phipps- FUDECI Exped. by American Mus. Nat. Hist., D. A. Grimaldi (AMNH).

Paravelia paolettii, new species

Figs. 9–14, 19

Description. Macropterous male: Ground color blackish brown, venter somewhat lighter; pronotum without anterior transverse band. Head orange-red, with a few small yellowish dorsal spots; distal ends of antennal tubercles, bucculae yellowish; rostrum yellow brown, darker distally. Legs, antennae dark brown except antennal segment 1 basally lighter. Head short, declivant anteriorly; bucculae prominent, short (Fig. 11); length of head 0.58; width of eye/interocular space, 0.20/0.53. Pronotum long, humeri prominent; weakly carinate on midline, carina evanescent posteriorly; set with shallow poorly defined pits; disc raised; posterior margin rounded distally; length : width, 1.88:1.85. Length of hemelytra from basal angle to apex, 7.00.

Dorsum clothed with short semi-erect pubescence, hemelytra without setae except along lateral margins. Abdominal venter not modified, bearing short appressed setae. Legs, antennae thickly clothed with short to moderate length setae, without long setae. Posterior trochanter unarmed. Middle femur medially set beneath with 3 small spines or denticles, increasing in length distally. Posterior femur denticulate from base to distal ⅔, denticles increasing in length distally, distal spine somewhat offset posteriorly. Posterior tibia beneath unarmed. Claws small, only slightly preapical; downcurving arolia of hind tarsi not visible.



Figs. 15–17. *Paravelia recens* Drake & Harris. 15. Male clasper or paramere (Brazil). 16. Male clasper or paramere (Bolivia). 17. Habitus, partial.

Antennal formula I:II:III:IV; 0.80:0.56:0.56:0.56.
Proportions of legs as follows:

	femur	tibia	tarsal 1	tarsal 2	tarsal 3
Anterior	1.55	1.33	0.08	0.20	0.33
Middle	1.83	1.80	0.05	0.30	0.33
Posterior	2.25	2.80	0.08	0.45	0.43

Abdominal sternite VII unmodified. Abdominal terminalia as shown in figure 10. Proctiger with a small median dorsal tubercle (Fig. 14); paramere long, distally truncate (Fig. 13).

Length, mean = 5.25 mm, N = 1.

Width, mean = 1.92 mm, N = 1.

Apterous male, Apterous female, Macropterous female: Unknown.

Material examined. Holotype, macropterous male: VENEZUELA: Aragua: Parque [Nacional Henri] Pittier, Rancho Grande, bromeliads, BR-3-tree 2, January 1988, M. G. Paoletti (JTPC). In the same sample was also 1 immature.

Etymology. This species is named for the collector of the only known specimens of this species, Dr. M. G. Paoletti.

Discussion. This species is most closely related to *Paravelia helenae* (Hungerford) but is larger and the armature of the legs is less well developed. The buccula of *P. paolettii* has a broad deep fovea (Fig. 11), while in *P. helenae* the same fovea is much smaller. These species share the following characters: striking orange-red and black coloration with contrasting light colored spots on the dark hemelytra; middle femur and hind femur denticulate ventrally; habitat in bromeliad water pockets. In *P. paolettii* the head is orange-red, the entire body black, and the entire basal angle of the hemelytra is yellow, whereas in *P. helenae* the head and body are orange-red, the

hemelytra black, and a basal spot on the hemelytra is white and separated from the base; both have a distal ovate light spot on the hemelytra.

Paravelia recens (Drake & Harris)
Figs. 4–8, 15–17, 19

Velia recens Drake & Harris 1935:192. Holotype, macropterous male, Panama, USNM.
Velia recens, Drake & Maldonado 1952:48. Habitat notes; distributional records, British Honduras (Belize), Venezuela.
Velia recens, Drake & Hussey 1954:133. Habitat notes; distributional records, Brazil, Guyana.
Paravelia recens, Polhemus 1976:512. New combination.
Paravelia recens, J. & D. Polhemus 1984:341, Fig. 6. Comparison with *P. manausana,* male paramere; distribution, Brazil.

Discussion. Because of morphological differences between populations of this species, we originally thought that several species were involved, however the characters we studied seem to vary independently, and major features such as head shape and femoral armature are quite constant. We examined details of the parameres, proctiger and first genital segment, the complement of denticles on the head and prosternum, the coloration of the pronotum, the shape and position of the light areas on the hemelytra, the relative lengths of the antennae, legs and tarsal segments, and the details of the male abdominal venter in an effort to clearly delineate separate taxa within the material at hand. We conclude that whereas there are differences between populations, we are most likely dealing with a single very widespread, and somewhat variable species.

Considering its apparently obligate restriction to bromeliad water pockets, the range of *P. recens* is remarkable, extending from Honduras to Bolivia. It has been found in both terrestrial and arboreal bromeliads belonging to a number of different genera and species, and therefore appears to be a generalist in regard to host choice. For a further description of habitats in which this species occurs see the discussion under *P. manausana.*

Drake and Maldonado (1952) noted that they had seen specimens of *P. recens* from British Honduras, but this may have been an error since the Drake collection contains only specimens from Honduras proper.

Material examined. BOLIVIA: Dept. La Paz: many males and females, Rio Coroico gorge, 28 km W Caranavi, bromeliads on cliffs, Cl 2523, 15 November 1989, J. T. & D. A. Polhemus (IELB, JTPC). BRAZIL: Amazonas: 2 males, 2 females, Cachoeira, Rio Cuieiras, A 76, 16 December 1960, E. J. Fittkau (erroneously listed as paratypes of *P. manausana* by Polhemus and Polhemus, 1984) (ZSMC, JTPC); 1 male, 1 female, Manaus, A-439, Rio Branco, 4 December 1969, E. J. Fittkau (JTPC); 3 males, Rio Negro, A-405, Rio Taruma, 11 November 1962, E. J. Fittkau (JTPC); 5 males, 6 females, nr. Manaus, Reserva Ducke, Ig. Acará, bromeliads on forest floor [*Vriesia splitgerberi*?], Cl 2476, 26 August 1989, J. T. & D. A. Polhemus (INPA, JTPC); Pará: many males and females, Belém, Rio Guamá, ex tank of bromeliad, 21 November 1973, R. T. Schuh (AMNH, JTPC); many males and females, 18 km E Belém, Marituba, ex tank of *Aechmea fulgens* (Bromeliaceae), 2 July 1974, R. T. Schuh (AMNH, JTPC). COLOMBIA: Chocó: 2 winged males, 2 winged females,

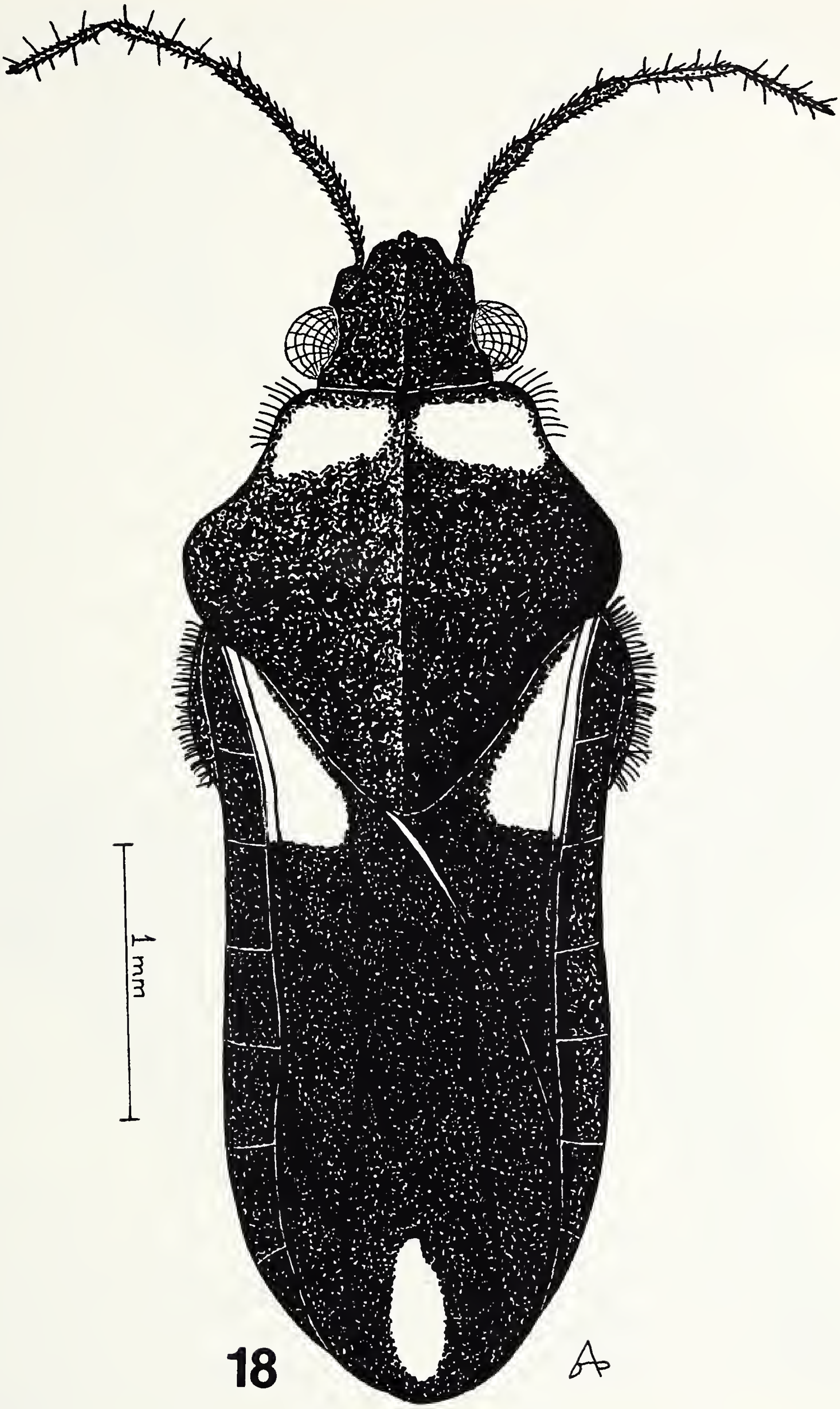


Fig. 18. *Paravelia manausana* J. & D. Polhemus. Dorsal habitus (legs omitted).

Charombirá, associated with *Anopheles* sp. in bromeliads, C. Murillo (UDVC). GUYANA: 1 male, 1 female, Bartica Triangle, ex bromeliads on mangrove, October 1948 to March 1949, D. J. Atkinson (JTPC). HONDURAS: 1 male, 1 female, Tela, 6 April [year?], T. H. Hubbell (JTPC). PANAMA: Canal Zone: 1 male, Monte Sirio,

Fig. 19. Distribution of bromeliadicolous *Paravelia* species. △ = *P. helenae.* □ = *P. manausana.* ○ = *P. recens.* ▽ = *P. paolettii.*

Fig. 20. Distribution of bromeliadicolous *Microvelia* species. △ = *M. distanti.* □ = *M. oaxacana.* ○ = *M. ancona.* ▽ = *M. laesslei.*

Gatuneillo River, 1956, C. J. Drake (holotype, USNM). PARAGUAY: Dept. Paraguari: 1 male, 1 female, Cerro Acahay, Area rocosa norte de la Cumbre Occidental, 550 m, on bare rock or among many stones, in spiny bromeliad, 30 May 1985, K. A. Kochalka (USNM). PERU: Dept. Pasco: several males and females, Pan de Azucar, 13 July 1961, F. S. Truxal (LACM, JTPC). VENEZUELA: Terr. Fed. Amazonas: 2 males, 2 females, Mt. Marahuaca, N. slopes, Benitez Camp, 1–25 May 1950, J. Maldonado Capriles (JTPC).

Microvelia ancona Drake & Chapman
Fig. 20

Microvelia ancona Drake & Chapman 1954:153. Holotype, macropterous female, Panama, USNM.

Discussion. This species was known only from the female type until several more recently collected series provided apterous forms. In the latter, the bright silvery pubescent areas on the abdominal tergites contrast with the velvety black ground color.

Material examined. COLOMBIA: 1 macropterous male, Chocó, Charambiro, January 1985, R. Astaiza (JTPC). ECUADOR: Napo: 8 apterous males, 3 macropterous males, 5 apterous females, 1 macropterous females, Baeza, 1,900 m, ex tanks of *Aechmea* (?) sp. (Bromeliaceae) (#69), 4 February 1976, R. T. Schuh (AMNH, JTPC). VENEZUELA: Aragua: many apterous and macropterous males and females, Parque [Nacional Henri] Pittier, Rancho Grande, bromeliads, January 89, M. G. Paoletti (JTPC).

Microvelia distanti Lundblad
Fig. 20

Microvelia insignis Distant 1912:437, Pl. X. Holotype, macropterous, sex unknown, El Tucuché, Trinidad, BMNH. Preoccupied by *Microvelia insignis* (Distant) 1903 (originally described in *Rhagovelia*).

Microvelia distanti Lundblad 1933:286. New name.

Microvelia distanti, Drake & Hussey 1954:134. Additional description, based on specimens from the type-locality.

Discussion. This species is apparently common in bromeliads on the summit of El Tucuché in Trinidad. It was also recorded from Dominica by Distant (1912). The record from Venezuela is from very close to the Brazilian border, and a considerable range extension. Spangler and Spangler (in press) provide additional detailed information on the biology of this species at the Cerra de la Neblina locality.

Material examined. TRINIDAD: 1 apterous male, 1 macropterous male, Mt. Tucuché, 2 February 1929, J. G. Myers (BMNH, JTPC). VENEZUELA: Terr. Fed. Amazonas: many apterous specimens, Cerro de la Neblina, Camp VII, 1,850 m, 30 January to 10 February 1985, on water in *Brocchinia tatei* (large bromeliad), P. J. & P. M. Spangler, R. A. Faitoute (USNM, JTPC).

Microvelia laesslei Drake & Hussey
Fig. 20

Microvelia laesslei Drake & Hussey 1954:134. Holotype, micropterous male, Jamaica, USNM.

Material examined. JAMAICA: 1 micropterous male, 1 macropterous male, Jaun de Bolas 2,500′, from bromeliads, 1–7 August 1952, A. M. Laessle (paratypes, JTPC); 3 micropterous males, 1 micropterous female, 3 nymphs, St. Ann Mt., Diablo For. Res., ex bromeliad, 14 July 1960, T. H. Farr (JTPC).

Microvelia oaxacana Drake
Fig. 20

Microvelia oaxacana Drake 1951:37. Holotype, apterous male, Mexico, Oaxaca, USNM.

Microvelia oaxacana, Drake & Hussey 1954:136. Description of macropterous form; distributional record, Mexico, D. F.

Microvelia oaxacana, Smith 1980:340. Distributional records, Chiapas and Puebla, Mexico.

Discussion. The specimens examined by Drake were all interceptions at border stations, and *Tillandsia* was the only named associate, the others simply given as "bromeliads." During a 1964 expedition to Mexico, J. T. and M. S. Polhemus collected a number of specimens from large broad leaved bromeliads growing on the horizontal limbs of large oak trees near Montebello Lakes in Chiapas. It was necessary to cut off the base of the plant and peel the leaves away to find the insects.

Material examined. MEXICO: Chiapas: 4 apterous males, 1 apterous female, 1 nymph, Montebello Lakes, ex bromeliads, CL 1082, 3 May 1964, J. T. & M. S. Polhemus (JTPC); Morelos: 1 apterous female, 6.3 mi N Cuernavaca, 29 July 1963, M. G. Naumann (JTPC); Puebla (?): Pueblo (sic), many apterous and macropterous specimens, 4,600 ft, 27 June 1953, I. Shenick (SEMC, JTPC).

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DISTRIBUTIONAL DATA AND NEW SYNONYMY FOR SPECIES OF *HALOBATES* ESCHSCHOLTZ (HETEROPTERA: GERRIDAE) OCCURRING ON ALDABRA AND NEARBY ATOLLS, WESTERN INDIAN OCEAN

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Abstract.—Five species of *Halobates* are recorded from the atolls of the Aldabra group: *H. germanus, H. micans, H. alluaudi, H. poseidon,* and *H. flaviventris.* These species are keyed, the variability of the populations inhabiting Aldabra and Cosmoledo atolls discussed, and notes provided on their ecological preferences. *Halobates eschscholtzi* Herring 1961 is placed as a junior synonym of *Halobates flaviventris* Eschscholtz 1822 (new synonymy).

During an expedition to Aldabra atoll in March and April of 1989 the first author was able to make extensive collections of *Halobates* in the western Indian Ocean, which revealed unsuspected range extensions and previously undocumented levels of intraspecific variation in several species. This report is an outgrowth of those studies, and is intended as a faunistic contribution covering the *Halobates* species occurring on the small islands and atolls lying between the granitic Seychelles and Madagascar in the northwest quadrant of the Indian Ocean, particularly those of the Aldabra group. Since the last revision of *Halobates* by Herring (1961), the only significant papers dealing with the Indian Ocean have been those of Cheng (1974) and Polhemus and Cheng (1982). The first of these discussed the distributions of *H. flaviventris, H. micans,* and *H. germanus* around the island of Nosy Be and on offshore seas north of Madagascar, while the second provided new records for *H. poseidon* and *H. flaviventris* along the east coast of Africa. The atolls of the western Indian Ocean have been essentially overlooked in terms of their *Halobates* fauna, and since no regional treatment exists a key to their species is provided below. The key and discussions should be applicable to species occurring among the islands ringing the southern margin of the Somali Basin (see Fig. 1), including the following areas: the granitic Seychelles, the Amirantes (African Islands, Desroches, Poivre, Noeufs, Alphonse), Platt, Coetivy, Providence-Cerf, St. Pierre, Farquhar, Agalega and the Aldabra group (Aldabra, Assumption, Astove, Cosmoledo). The *Halobates* fauna of the Comores is essentially unknown, but should also contain many of these species. Additional endemic species not treated herein occur in Madagascar, the Mascarenes, along the eastern coast of Africa, and in the Red Sea.

The five species of *Halobates* recorded from Aldabra and Cosmoledo represent

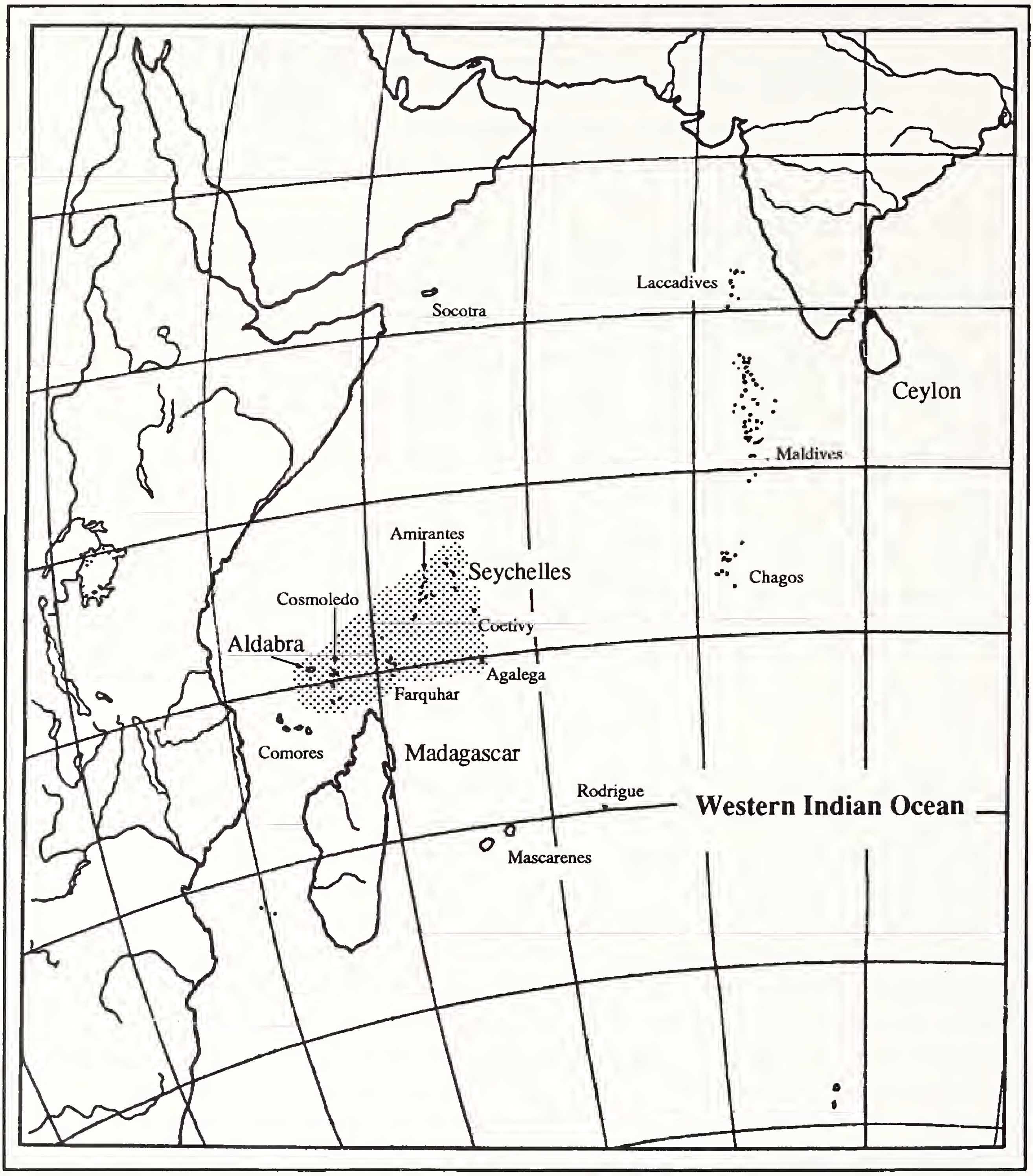

Fig. 1. Area of the western Indian Ocean covered by this work. The sizes of the small islands and atolls on the map have been exaggerated for the sake of resolution.

the greatest species diversity known from any coral atolls in the Indo-Pacific region. This species richness is likely due to the fact that these islands are raised, cliff-bound atolls which provide a wide range of reef, lagoon and mangrove habitats. The atolls harbor no endemic species, but the populations present on them often exhibit distinctive intraspecific variations in color pattern and setiferation which are indicative of incipient speciation (see further discussion below). Of the five species present, two (*micans* and *germanus*) are widespread pelagic species, one (*flaviventris*) is present in nearshore habitats throughout the Indo-Pacific, one (*alluaudi*) is shared with the

granitic Seychelles, and one (*poseidon*) is shared with east Africa. These atolls thus appear to have been colonized by *Halobates* species which have arrived from several different directions, and seem to lie in a contact zone between species assemblages typical of both the western and eastern portions of the Indian Ocean.

The local distribution and habits of species occurring on Aldabra atoll will be covered in far more detail by the first author in a forthcoming publication (D. Polhemus, in press), and the localities listed herein are only those which establish new distribution records. For a recent review of basic *Halobates* biology, ecology and distribution readers are referred to Cheng (1985). All material cited was collected by D. A. Polhemus and is deposited in the National Museum of Natural History, Washington, D.C. (USNM) along with many additional specimens not discussed below. Synoptic series are also held in the J. T. Polhemus collection, Englewood, Colorado (JTPC).

In the material examined sections, the names of individual islets making up the outer rings of Aldabra and Cosmoledo atolls are listed in bold face. CL numbers following localities refer to a numbering system used to reference ecological notes. The latitudes and longitudes given were determined by use of a Satnav global positioning system.

KEY TO THE SPECIES OF *HALOBATES* OCCURRING IN THE ALDABRA GROUP AND NEARBY ATOLLS, WESTERN INDIAN OCEAN

1a. Width of head between the eyes greater than its length; interocular width about 4 times the width of an eye; body usually unicolorous silvery grey, lacking extensive yellow or brownish markings on the thoracic and abdominal venter or on the dorsum of the head; open ocean species 2

1b. Width of head between eyes less than its length; interocular width distinctly less than 4 times the width of an eye; body marked with yellow or brownish on the abdominal and thoracic venter, and usually on the dorsum of the head (either as a posteriorly convex crescent-shaped mark or as a broad patch isolating an arrow shaped dark mark centrally); nearshore species 3

2a. Smaller species, length of male less than or equal to 4.00 mm, length of female less than or equal to 3.80 mm; male left styliform process not bent upwards, lying horizontally in lateral view; male tergite IX with patches of black bristles on lateral wings (see figs. 7–9 in Herring, 1961) .... *germanus*

2b. Larger species, length of males greater than or equal to 4.40 mm, length of females greater than or equal to 4.00 mm; male left styliform process bent abruptly upwards, appearing vertical in lateral view; male tergite IX lacking patches of black bristles on lateral wings (see figs. 1–3 in Herring, 1961) .... *micans*

3a. Foreleg with length of tarsal segment I longer than or equal to length of tarsal segment II (for male genitalia see figs. 73–75 in Herring, 1961) .... *alluaudi*

3b. Foreleg with length of tarsal segment I distinctly shorter than length of tarsal segment II 4

4a. Foreleg with length of tarsal segment I less than or equal to ⅔ the length of tarsal segment II; male left styliform process not bent outward or visible from above (see figs. 52–54 in Herring, 1961) .... *poseidon*

4b. Foreleg with length of tarsal segment I greater than ⅔ the length of tarsal segment II; male left styliform process bent outward, visible from above (see figs. 85–87 in Herring, 1961) .... *flaviventris*

Halobates germanus White

Halobates germanus White 1883. Voyage Challenger, Rept. Zool. 7(19):50, pl. 1, fig. 6. [Type-locality given as "North Pacific Ocean."]

Discussion: This moderate sized pelagic species is widely distributed in the Indian and western Pacific oceans (see Andersen, 1982, pg. 370, fig. 629). The species was known previously from the coasts of Africa and Arabia, but had not been recorded from any atoll in the western Indian Ocean. At Aldabra *H. germanus* was always found on open seas at least 1,000 meters offshore, in company with *H. micans.*

Material examined: ALDABRA ATOLL, **Grande Terre**: 1 male, 1 female, open sea 1,000 m offshore of Dune Jean Luis, 9°27′94″S, 46°25′92″E, 11:30 hr, sea temp. 28°C., 8 March 1989 (USNM). **Malabar**: 2 males, 4 females, net tow on calm sea 1,000 meters offshore from Passe Gionnet to Passe Houareau, 12 March 1989, 09:00 hr, CL 8032 (USNM). COSMOLEDO ATOLL, **Menai**: 1 male, 1 female, calm sea 500 meters offshore of Johannes Point settlement site, 9°41′68″S, 47°32′26″E, 13:00 hr, 27 March 1989, CL 8041 (USNM).

Halobates micans Eschscholtz

Halobates micans Eschscholtz 1822. Entomographien 1:107, pl. 2, fig. 3. [Type-locality given as "Im sudlichen stillen Meere und im sudlichen atlantischen Meere"; types presumably in University of Dorpat.]

Discussion: This silvery, moderate sized pelagic species is widely distributed throughout all the tropical oceans of the world (see Andersen, 1982, pg. 370, fig. 629). As with *H. germanus,* this pelagic species was always found at least 1,000 meters offshore at Aldabra Atoll, and was never observed in the lagoon. Several collections of this species were also made on the open sea during the voyage to and from Aldabra. It was observed that the insects seemed to prefer the calm patches of water that often appeared on the otherwise slightly disturbed sea surface, and would rest in these in the same way that a freshwater species might use a sheltered eddy in a stream.

Material examined: ALDABRA ATOLL, **Grande Terre**: 2 males, 2 females, open sea 1,000 m offshore of Dune Jean Luis, 9°27′94″S, 46°25′92″E, 11:30 hr, sea temp. 28°C, 8 March 1989 (USNM). COSMOLEDO ATOLL, **Menai**: 2 females, on calm sea 1,000 meters offshore of northeast tip, 18:00 hr, 27 March 1989 (USNM). INDIAN OCEAN, **Somali Basin**: 5 males, 2 females, 5 immatures, 8°59′62″S, 48°33′28″E, 28 March 1989, on calm sea, 07:00 hr (USNM); 2 males, 3 females, 1 immature, 8°21′87″S, 49°32′23″E, 29 March 1989, on sea with light swell, 18:30 hr (USNM); 2 males, 1 female, 1 immature, 7°44′20″S, 50°26′39″E, 30 March 1989, on sea with moderate swell, 07:30 hr (USNM); 1 male, 7°6′78″S, 51°20′75″E, 30 March 1989, 18:00 hr (USNM).

Halobates alluaudi Bergroth

Halobates alluaudi Bergroth 1893. Rev. Ent. Caen 12:204. [Type-locality Seychelles Islands; types in Paris Museum according to Herring (1961).]

Discussion: This large silvery species is a strong and agile skater that appears to prefer the shelter of rocky shores. In the granitic Seychelles males of this species were

common in the nearshore shallows, while females skated on deeper water at much greater distances from shore and were difficult to capture without the aid of a boat. At Aldabra *H. alluaudi* occurred both in the lagoon and on the outer coasts of the atoll; individuals were observed skating against the incoming tidal current in the lagoon passes, in a manner analogous to freshwater gerrids holding station against the current on freshwater streams.

The material from both Aldabra atoll (males and females) and Cosmoledo atoll (males only) matches very well with topotypic specimens from the granitic Seychelles except that the females from Aldabra either entirely lack black setae on the mesonotum or have only a small scattering of short black setae on the anterior part, whereas in females from the granitic Seychelles the mesonotum is thickly covered with stiff black setae. The Aldabra females also possess fore femora that are light colored beneath, while in the populations on the granitic islands the fore femur is dark beneath. Both of these are key characters used by Herring (1961) in his monograph of the genus. The males from all three localities are the same in all important respects, thus we have concluded that all of our material belongs to *alluaudi.* The atoll populations have apparently genetically fixed slight differences that in our opinion do not constitute separate species characters.

Distant (1913) recorded this species from Mahe, Aldabra, Coetivy, the Amirantes, the Chagos Archipelago, and Port Sudan in the Red Sea. It is likely that Distant's species concept was broader than the modern interpretations of later authors, and his Red Sea and Chagos records should be considered questionable until the specimens upon which they were based can be examined. Coetivy and the Amirantes, would seem to fall logically into the known range of the species, but these low sandy islands do not provide the type of habitat favored by *H. alluaudi,* which occurs almost exclusively along rocky shores, and is rarely encountered over 1,000 meters offshore. *H. alluaudi* frequently occurs in sympatry with *H. flaviventris,* a widely distributed species that tends to be found in open offshore waters, and the two species are superficially rather similar, being elongate and silvery. It thus seems possible that Distant's records of *H. alluaudi* from Coetivy and the Amirantes may be based on misidentified specimens of *H. flaviventris.*

Material examined: ALDABRA ATOLL, **Picard**: many males and females, rocky islets and mangrove clumps of *Sonneratia alba* at La Gigi, near Passe Femme, CL 8027, 11 March 1989 (USNM, JTPC). COSMOLEDO ATOLL, **Menai**: 5 males, calm sea 500 meters offshore of Johannes Point settlement site, 9°41′68″S, 47°32′26″E, 13:00 hr, CL 8041, 27 March 1989 (USNM). SEYCHELLES, **Mahe**: 17 males, 1 female, along rocky granite coast at Port Glaud, L'Islette Bay, CL 8043, 1 April 1989 (USNM, JTPC).

Halobates poseidon Herring

Halobates poseidon Herring 1961. Pac. Ins. 3:287. [Type-locality Mombasa, Kenya; holotype in British Museum (Natural History).]

Discussion: At Aldabra this small dark grey species was typically encountered along the margins of the lagoon, and frequently schooled in mangrove lined channels. Populations were also present in several limestone sinkholes in the interior of Picard

Island, which were flooded with seawater via subterranean passages but lacked any direct connections to the sea.

The material from Aldabra matches very well with specimens at hand from Kenya, Tanzania and Madagascar, however the Cosmoledo specimens exhibit a remarkable color shift, particularly in the females, wherein the central portions of the mesonotum and head are broadly infused with orange. Some Cosmoledo males have a more or less normal coloration, but all females have the distinctive orange pattern. We originally thought these populations must represent a new species, but all structural characteristics are the same as other populations of *poseidon,* thus we conclude that this is yet another example of genetic drift in an isolated population.

Material examined: ALDABRA ATOLL, **Grande Terre**: many males and females, mangrove estuary lined with *Avicennia marina* at upper end of L'Eglise Channel, off Takamaka Arm, 14 March 1989, CL 8031 (USNM, JTPC). **Picard**: 8 males, 5 females, Upsidedown Jellyfish Pool, nr. Aldabra Research Station, 9 March 1989, CL 8022 (USNM). COSMOLEDO ATOLL, **Menai**: many males and females, along sheltered sandy shore lined with *Avicennia marina,* on lagoon side across from Johannes Point settlement site, 9°41′68″S, 47°32′26″E, 27 March 1989, 10:00 hr, CL 8041 (USNM, JTPC).

Halobates flaviventris Eschscholtz

Halobates flaviventris Eschscholtz 1822. Entomographien 1:109, pl. 2, fig. 5. [Type-locality given as "Im sudlichen atlantischen Meere," doubted by Herring (1961); types presumably in University of Dorpat.]

Halobates eschscholtzi Herring 1961. Pac. Ins. 3:254 [Type-locality Zanzibar; holotype in British Museum (Natural History).] (New synonymy).

Discussion: This moderately large and elongate silvery species was usually found 100 to 500 meters offshore on the sheltered north and west coasts of Aldabra. In its habits it was intermediate between the open ocean forms and the nearshore species, with a behavior pattern similar to that observed for *H. princeps* White in the Malay Archipelago. Individuals would cruise outside of and parallel to the reef crest fringing the outer coasts, and were never observed in the lagoon.

Herring described *H. eschscholtzi* from females taken at Zanzibar, placing it in his open ocean group on the basis of a wide interocular space "approximately 4 × width of an eye," and comparing it with *H. micans* Eschscholtz and *H. splendens* Witlaczil. We have studied one paratype, somewhat teneral, that agrees with his description, and find that his placement of this species in the open ocean group is not correct. The apparently wide interocular space/width of eye ratio is due to a slight shrivelling of the eyes, and the ventral abdominal segments have yellowish areas, so that actually the species should be placed with those species that occur near shore. With females and males now available from Aldabra and Cosmoledo atolls, as well as Tanzania, it becomes evident that *eschscholtzi* is a synonym of *flaviventris.* We have specimens of *flaviventris* from the New Hebrides and Palau that are slightly smaller than those from the western Indian Ocean and have a narrower interocular space, as well as intermediate forms from Ceylon, thus it appears that there is a clinal pattern for this character across the Indo-Pacific region associated with variations in body size.

Material examined: ALDABRA ATOLL, **Picard**: 2 males, net tow 100 meters

offshore of rocky coast from Research Station to Grande Passe, 16 March 1989 (USNM). **Polymnie**: 2 males, in net tow 30 m offshore of north coast from Grande Passe to Passe Gionnet, CL 8034, 16 March 1989 (USNM). **Malabar**: 2 males, net tow on calm sea 1,000 meters offshore from Passe Gionnet to Passe Houareau, 12 March 1989, 09:00 hr, CL 8032 (USNM). COSMOLEDO ATOLL, **Menai**: 1 male, 3 females, calm sea 500 meters offshore of Johannes Point settlement site, 9°41′68″S, 47°32′26″E, 13:00 hr, 27 March 1989, CL 8041 (USNM).

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A NEW GENUS OF MIRINE PLANT BUGS, *GRACILIMIRIS*, WITH THREE NEW SPECIES FROM NORTH AMERICA (HETEROPTERA: MIRIDAE)

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Abstract.—The new mirine genus *Gracilimiris* and the new species *G. litoralis,* from the eastern United States, and *G. strigosus* and *G. wheeleri* from Arizona and Texas are diagnosed and described. All three species are associated with grasses (Poaceae). Male genitalia of all species are figured and a dorsal habitus is provided for the male of the type species, *G. litoralis.* Scanning electron micrographs are presented for the dorsal setae, scent gland ostiole, and pretarsus of *G. strigosus.*

Our studies of the genus *Phytocoris* Fallén in North America (Henry and Stonedahl, 1983; Stonedahl, 1988) revealed three undescribed species of the tribe Mirini that could not be placed in any known genus. Although similar to some species of *Phytocoris* in external appearance, the male genital structures of these taxa are sufficiently distinct to warrant their placement in a new genus. The unique combination of external diagnostic features supports this placement.

All measurements are given in millimeters. Abbreviations used in the locality data to denote specimen depositories correspond to the institutions listed in the acknowledgments.

Gracilimiris, new genus

Diagnosis. Recognized by the elongate body form (Fig. 1); head with anteriorly prominent frons and strongly produced base of tylus (Fig. 2); long first antennal segment with dense brush of stout setae ventrally (Fig. 3); flattened pronotal collar; carinate lateral margins of pronotum; and characters of the male genitalia, particularly the prominent, asymmetrical posteroventral region of the genital capsule (Fig. 8f) and structure of the parameres (see description of genitalia).

Description of macropterous male. Elongate, total length 4.64–7.03; general coloration brownish yellow or grayish yellow, with limited brown to fuscous markings; dorsal surface smooth or very faintly roughened, slightly shining, veins of hemelytra weakly elevated; dorsal vestiture with short to moderately long, golden brown to dark brown, suberect, bristlelike setae and recumbent, silvery white, sericeous setae (Fig. 7); thoracic pleura and abdominal venter with dense distribution of sericeous setae. **Head.** Subquadrate, slightly broader than long, weakly convex dorsally, well produced anteriad of antennal fossae in dorsal view; vertex slightly broader than width of one eye; frons noticeably produced anteriorly, projecting over base of tylus,

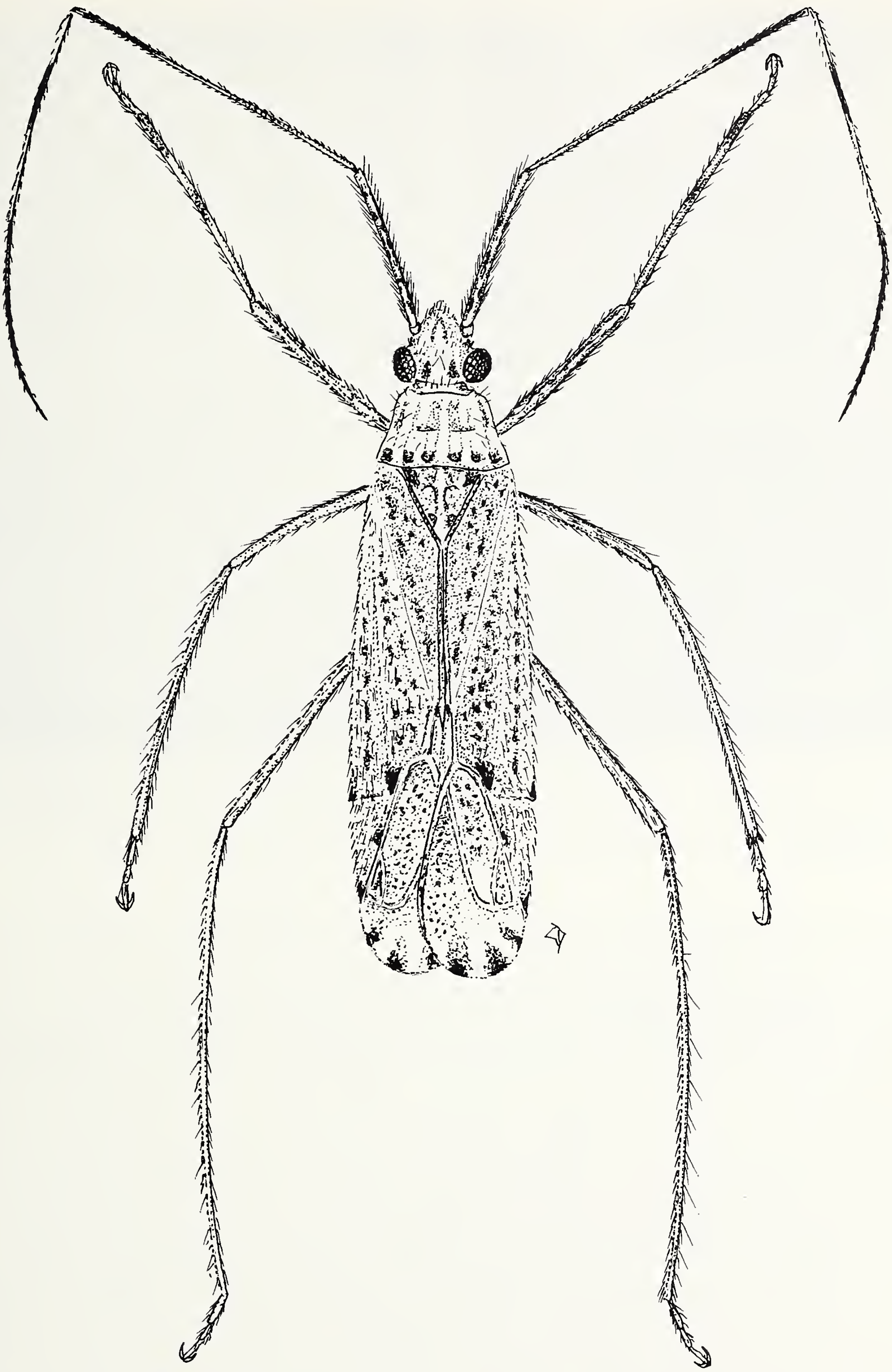
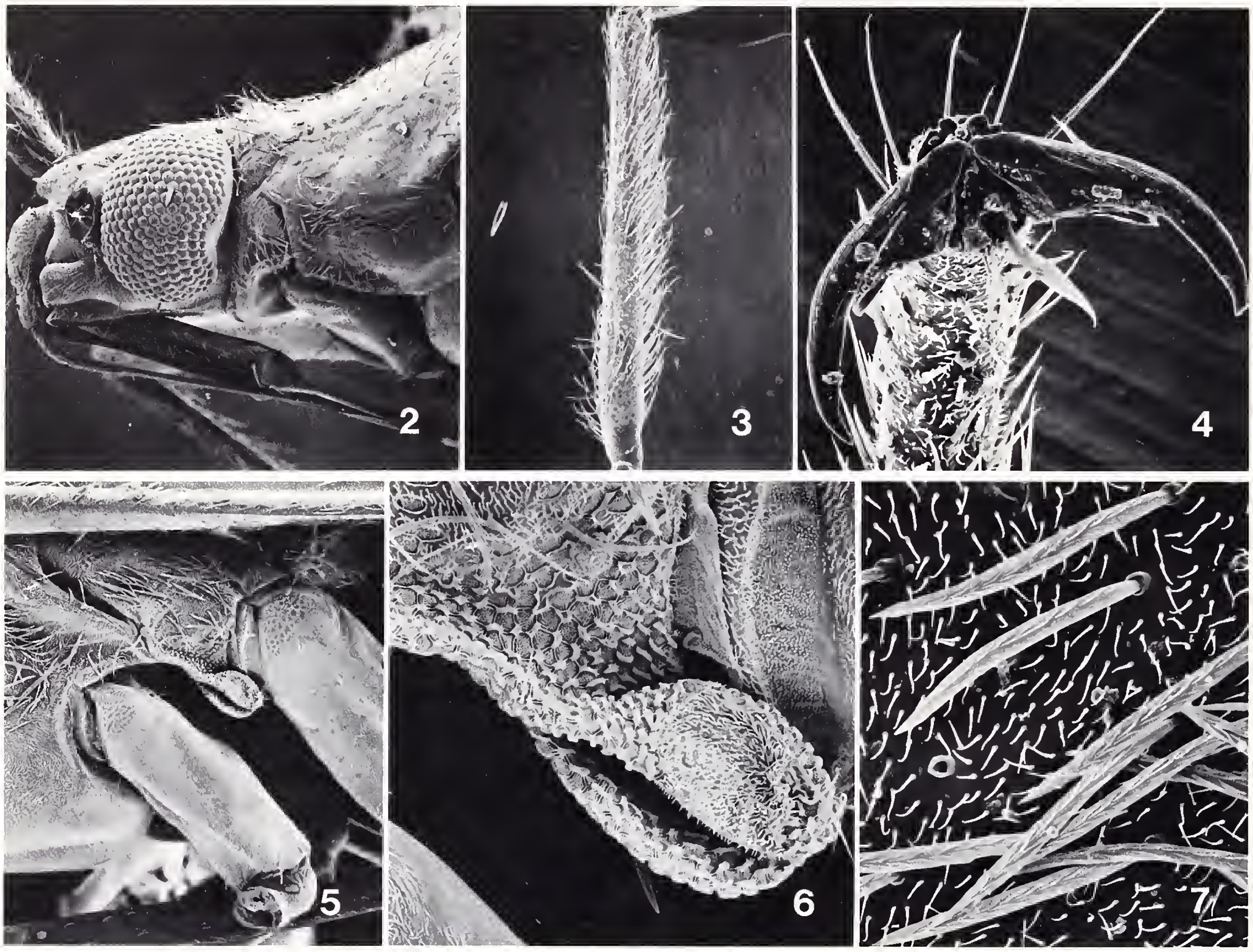


Fig. 1. *Gracilimiris litoralis,* dorsal habitus, ♂.



Figs. 2–7. Scanning electron micrographs of *Gracilimiris strigosus*. 2. Lateral view of head. 3. Antennal segment I. 4. Pretarsus. 5. Lateral view of thorax. 6. Ostiole and evaporative area of metathoracic scent efferent system. 7. Sericeous setae on hemelytra.

juncture with tylus strongly depressed (Fig. 2); tylus prominent, slightly bulbous basally, narrowing distally; lora quadrate, moderately inflated; gula well developed; eyes occupying most of height of head in lateral view, projecting laterally to slightly beyond anterolateral angles of pronotum in dorsal view; posterior margin of eye contiguous with anterior margin of pronotum; antenna inserted near median level of eye, fossa nearly contiguous with anterior margin of eye; antennal segment I linear or very slightly broadened basally, length equal to or greater than posterior width of pronotum, dorsal and lateral surfaces with long, pale setae (length of setae about equal to width of segment), ventral surface with dense brush of slightly longer setae; antennal segments II–IV linear, with fine, reclining setae, segment II usually with several longer, suberect setae; labium extending between metacoxae or slightly beyond. **Pronotum.** Trapezoidal in dorsal view; lateral margins weakly to strongly carinate posteriad of coxal cleft, carina becoming less prominent posteriorly (Fig. 2); posterior margin straight, or weakly and broadly convex with shallow concave region medially; posterior submargin with six weakly tumid scallops, each bearing a tuft of dark setae; anterior margin with flattened collar separated from remainder of pronotum by shallow suture which extends to lateral margins of pronotum; calli weakly elevated, narrowly separated medially, with shallowly depressed posterior borders; mesoscutum broadly exposed; scutellum weakly convex; ostiole and evaporative area

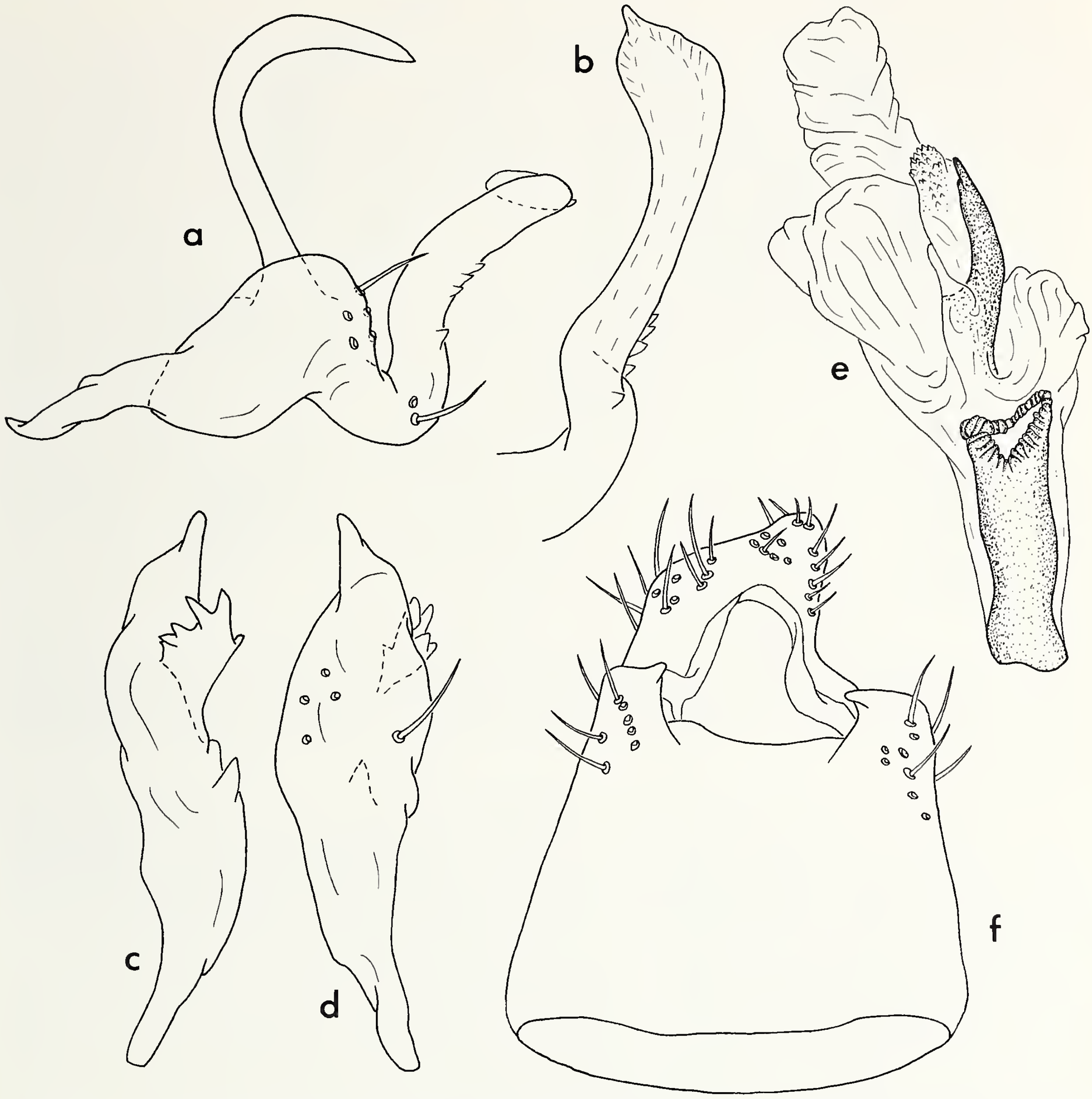


Fig. 8. a–f. Male genitalia of *Gracilimiris litoralis*. a. Left paramere, lateral view. b. Shaft of left paramere, dorsal view. c. Right paramere, dorsal view. d. Right paramere, lateral view. e. Vesica. f. Genital capsule, dorsal view.

of metathoracic scent gland as in Figures 5 and 6. **Hemelytra.** Elongate, subparallel, lateral margins straight or weakly rounded; length of cuneus 2.5–3.0 times basal width; apex of clavus and inner posterior angle of corium with tuft of dark, bristlelike setae; membrane lightly to densely conspurcate, spots usually coalescing to form larger dark marks distad of areolar cells. **Legs.** Femora elongate, hind pair strongly tapered, reaching beyond apex of abdomen; tibiae with four rows of dark (rarely paler) spines and dorsally with two irregular rows of tiny black spinules; tarsi elongate, segment I sometimes as long as segments II and III combined, segment II about half as long as segment III; pretarsus as in Figure 4. **Genitalia.** Genital capsule subquadrate, strongly produced and narrowed distad of paramere sockets (Fig. 8f), without tuberculate processes dorsad of sockets. Left paramere with prominent sensory lobe bearing large sickle-shaped process (Figs. 8a, 9a, 10a); shaft strongly elevated basally,

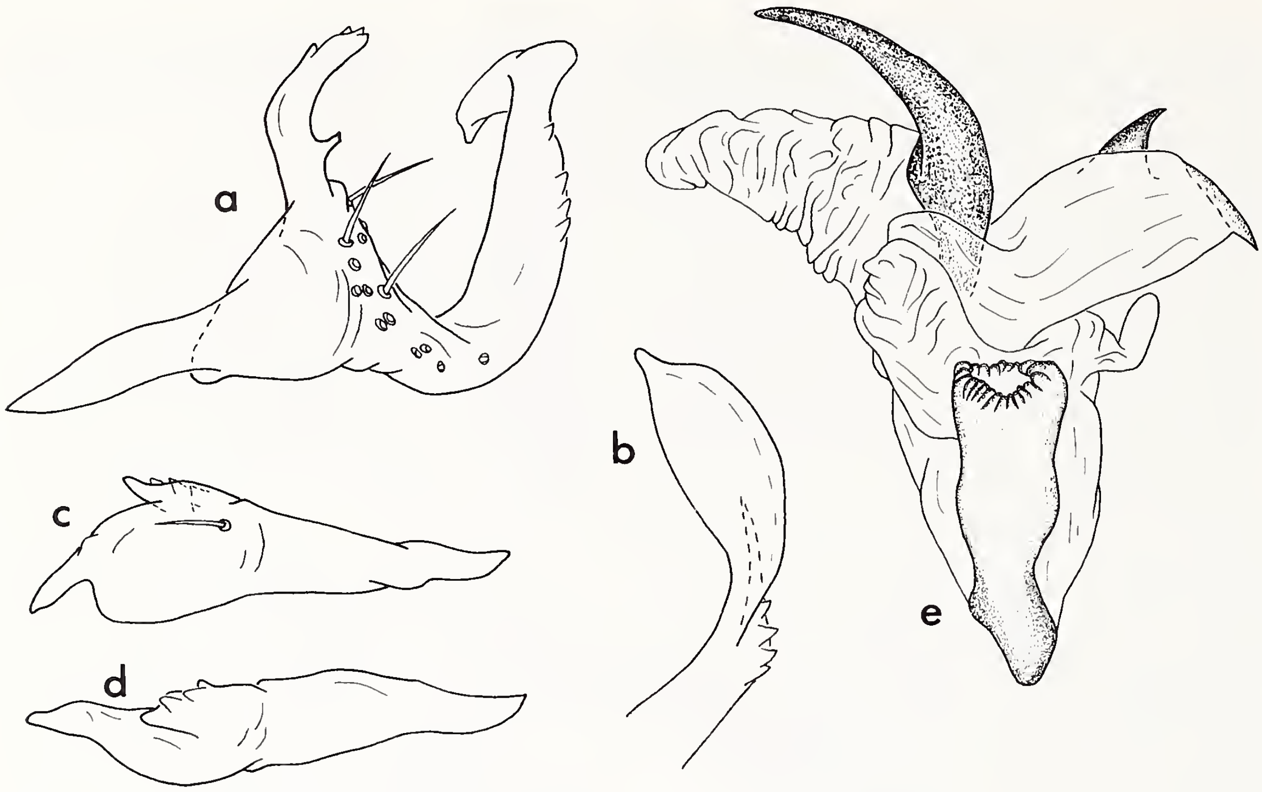


Fig. 9. a–e. Male genitalia of *Gracilimiris strigosus.* a. Left paramere, lateral view. b. Shaft of left paramere, dorsal view. c. Right paramere, lateral view. d. Right paramere, dorsal view. e. Vesica.

elongate, slightly expanded distally (Figs. 8b, 9b, 10b). Right paramere with prominent, toothlike process(es) on inner dorsal surface and at apex (Figs. 8c,d, 9c,d, 10c, d). Vesica with several membranous lobes and a single lobal sclerite process, lobes sometimes bearing a small sclerite or field of spines distally (Figs. 8e, 9e, 10e).

Female. Macropterous, submacropterous, or brachypterous. Head with smaller eyes and broader vertex than in male. Color and vestiture similar to male, except dorsum usually with fewer dark markings, and spots on hemelytral membrane sometimes restricted to region distad of areolar cells. Genitalia not examined.

Etymology. From the Latin, *gracilis* (slender, thin) and *miris,* referring to the slender body form; gender masculine.

Type species. Gracilimiris litoralis, new species.

Distribution. Arizona, west Texas, and the coastal eastern United States from Maryland to Florida and Texas.

Discussion. The relationships of the Mirini are not sufficiently known to allow us to determine with confidence the position of *Gracilimiris* relative to other genera of the tribe. Externally, the species of this genus resemble elongate species of *Phytocoris,* especially those placed in the *candidus* and *roseipennis* species-groups (see Stonedahl, 1988). In particular, the elongate body form with strongly tapered hind femora, subquadrate head with prominent frons, elongate first tarsal segment, and long first antennal segment with dense brush of long setae ventrally are characteristic of species placed in these groups of *Phytocoris.* None of the above external features are unique to *Gracilimiris* and *Phytocoris,* but occur in various combinations in other groups of Mirinae (e.g., *Alda* Reuter, *Eremobiellus* Reuter, *Euphytocoris* Poppius, *Miridius* Fieber, *Stenotus* Jakovlev, some Stenodemini). Clearly, a much broader survey of

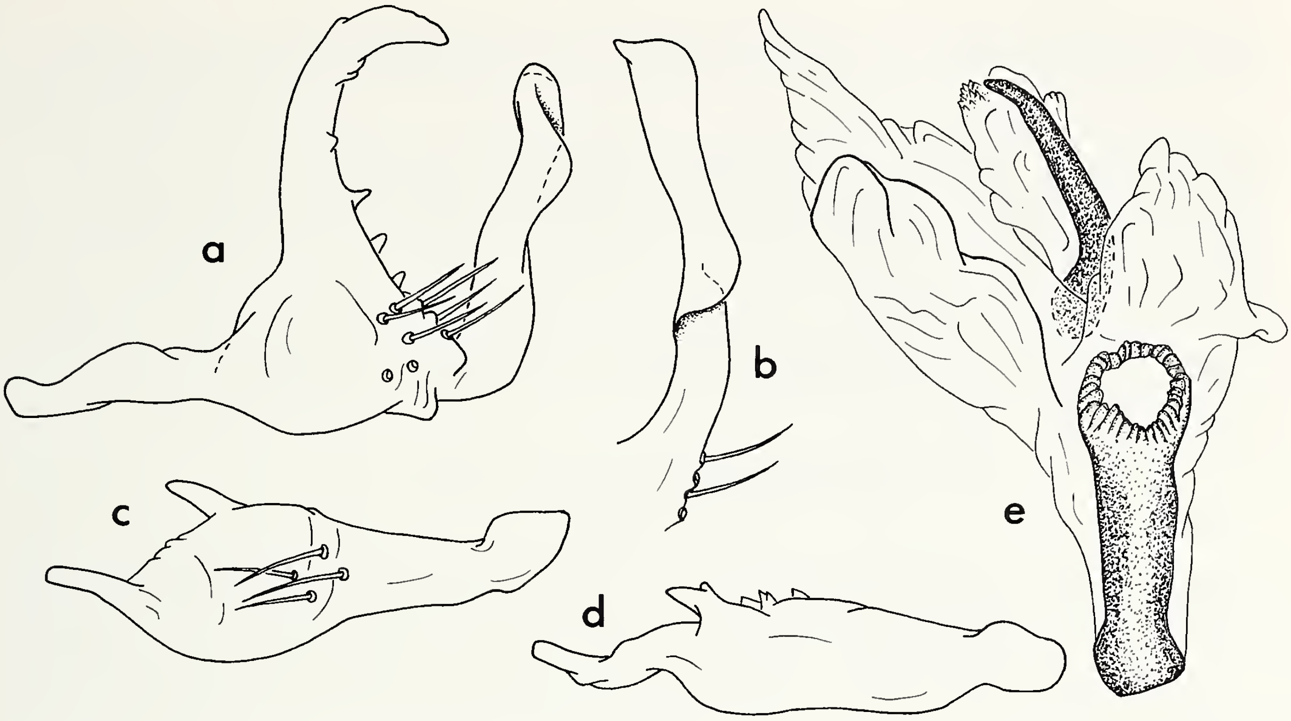


Fig. 10. a–e. Male genitalia of *Gracilimiris wheeleri*. a. Left paramere, lateral view. b. Shaft of left paramere, dorsal view. c. Right paramere, lateral view. d. Right paramere, dorsal view. e. Vesica.

taxa and characters is required to establish the relationships of *Gracilimiris* and other superficially similar mirine genera.

Other diagnostic features of the genus *Gracilimiris* include: (1) carinate lateral margins of pronotum, (2) flattened pronotal collar, (3) male genital capsule with strongly produced, asymmetrical, posteroventral region (Fig. 8f), (4) sensory lobe of left paramere with prominent, sickle-shaped process (Figs. 8a, 9a, 10a), and (5) right paramere with prominent toothlike processes on inner dorsal surface (Figs. 8c, d, 9c, d, 10c, d). Although the carinate pronotal margins and flattened collar are not unique features, we are unaware of any other Mirini that possess a genital capsule and parameres like those of *Gracilimiris* species. Some species of *Phytocoris* in the *aurora* group (Stonedahl, 1988) have a left paramere similar to that seen in *Gracilimiris,* but the shape and location of the process on the sensory lobe are different.

The host plant records for *Gracilimiris* species indicate that the genus is strictly associated with grasses (Poaceae). *G. litoralis,* has been collected on salt-meadow cordgrass, *Spartina patens* (Ait.) Muhl., a grass of coastal brackish marshes in the eastern United States, and *G. wheeleri* has been taken in Pima County, Arizona, on bush muhly, *Muhlenbergia porteri* Scribn. The only host record for *G. strigosus* comes from two specimens collected in Pima County, Arizona, on "grasses." All three species of the genus have been collected at light.

KEY TO SPECIES OF *GRACILIMIRIS*

1. Clavus and corium conspurcate (Fig. 1) with fuscous spots often surrounding bases of dark, bristlelike setae; antennal segment I marked with fuscous patches, sometimes coalescing to form dark stripes, or segment extensively darkened 2
– Clavus and corium without fuscous spots or dark bristlelike setae; antennal segment I

uniformly brownish yellow, sometimes suffused with darker brown but never with distinct fuscous patches or stripes; male genitalia as in Figure 10; Arizona and west Texas .... *wheeleri,* new species

2. Apical fourth of antennal segment II noticeably darker than remainder of segment, sometimes also slightly darker medially; antennal segment III pale with broad, dark band below middle (Fig. 1); tarsi uniformly pale or with segment III narrowly infuscated apically; male genitalia as in Figure 8; coastal eastern United States from Maryland to Florida and Texas .... *litoralis,* new species

– Antennal segment II uniformly brown or fuscous; antennal segment III dark brown, narrowly pale basally; tarsi uniformly fuscous; male genitalia as in Figure 9; Arizona and west Texas .... *strigosus,* new species

Gracilimiris litoralis, new species
Figs. 1, 8

Diagnosis. Recognized by the conspurcate hemelytra, strong carina on lateral margins of pronotum, head with two dark spots bordering inner posterior angles of eyes, apical fourth of antennal segment II noticeably darker than remainder of segment, antennal segment III pale with broad dark annulus below middle, and male genitalia as in Figure 8.

Description of male. Length 5.14–7.03; general coloration pale grayish yellow, with limited brown to fuscous markings. **Head:** Width across eyes 0.66–0.88, vertex 0.26–0.37; pale brownish yellow with limited reddish-brown markings on frons and vertex, and two large fuscous spots bordering inner posterior angles of eyes. **Antennae:** I, length 1.13–1.82, pale with dark spots dorsally and laterally, spots often coalescing into three fairly distinct dark stripes; II, length 2.26–3.28, brownish yellow, sometimes slightly darker medially, apical fourth fuscous, much darker than remainder of segment; III, pale with broad, fuscous annulus below middle; IV, dark brown. **Labium:** Length 2.16–2.59; extending between hind coxae or slightly beyond. **Pronotum:** Posterior width 0.91–1.24; collar and calli with brown or brownish-red markings; disc bordering lateral margins lightly to moderately suffused with fuscous, especially opposite calli; lateral margins of disc distinctly carinate; posterior margin nearly straight, but with broad, shallow concave region medially; lateral angles of mesoscutum darkened; scutellum marked with brownish red or fuscous on either side of pale median stripe, and with two large fuscous patches laterally before apex. **Hemelytra:** Conspurcate, spots on membrane slightly smaller than those on clavus and corium; posterior angles of corium and apices of clavus and cuneus with larger fuscous marks. **Legs:** Grayish yellow or brownish yellow with red to fuscous markings, these mostly arranged in longitudinal lines; fore tibiae usually with two or three dark annuli; tarsi uniformly pale or narrowly darkened at apex of segment III. **Genitalia:** Figure 8.

Female. Brachypterous (forewings extending to abdominal segment VIII), length 4.56, or submacropterous (forewings just surpassing apex of abdomen), length 5.09–5.24; color and vestiture similar to male, except dorsum tending to have fewer dark markings; head slightly narrower than in male with smaller eyes and broader vertex, width across eyes 0.70–0.78, width of vertex 0.38–0.47; length of antennal segment I 1.53–1.67, segment II 2.66–2.73; length of labium 2.34–2.55; posterior width of pronotum 0.98–1.06.

Etymology. From the Latin, *litoralis* (of the shore), referring to the occurrence of this species in shoreline habitats, where it is associated with grasses.

Distribution. Coastal areas from Crisfield, Maryland to Devers, Texas.

Holotype ♂. USA. **Florida.** *Dade Co.:* Paradise Key, Feb. 19, Schwarz and Barber '19 (USNM).

Paratypes. USA. **Florida.** *Duval Co.:* 1♂, Jacksonville, June 30, 1959, D. Ribble (KU); 1♀, Jacksonville Beach, Sept. 26, 1970, on brackish grasses, F. W. Mead (USNM). *Gulf Co.:* 1♀, Port St. Joe, May 8, 1982, swept from *Spartina* sp., T. J. Henry (USNM). *Highlands Co.:* 2♂, Sebring, Oct. 10–30, C. T. Parsons (AMNH). *Hillsborough Co.:* 2♂, 1♀, Tampa, Sept. 10, 1927, E. D. Ball (USNM). *Orange Co.:* 1♂, Winter Park, May 10, 1940, H. T. Fernald (USNM). *Volusia Co.:* 1♂, Rt. 415, 2 mi N of Osteen, April 27, 1984, T. J. Henry, J. T. Polhemus and A. G. Wheeler, Jr., taken at light (JTP). *County ?:* 1♂, coast between Stuart and St. Augustine, June 17–25, 1951, O. Bryant (CAS); 1♂, Yankeetown, July 7, 1948, B. T. McDermont (KU). **Maryland.** *Somerset Co.:* 1♂, Crisfield, Aug. 5, 1932, in mosquito trap, F. C. Bishop (USNM). **Mississippi.** *Hancock Co.:* 2♂, Pearlington, June 25, 1948, R. H. Beamer (KU). **North Carolina.** *Onslow Co.:* 2♂, Ashe Island, June 4, 1975 and Aug. 19, 1975, ex *Spartina patens* (Ait.) Muhl., J. C. Dukes (USNM). **Texas.** *Liberty Co.:* 1♂, Devers, June 22, 1917, H. H. Knight (USNM).

Additional specimens. USA. **Florida.** *Hillsborough Co.:* 2 nymphs, Tampa, Sept. 10, 1927, E. D. Ball (USNM). **Maryland.** *Somerset Co.:* 1♂ (damaged with hemelytra missing), Crisfield, Aug. 3, 1932, in mosquito trap, F. C. Bishop (USNM).

Gracilimiris strigosus, new species
Figs. 2–7, 9

Diagnosis. Very similar to *G. litoralis* in general appearance, but distinguished by the uniformly darkened tarsi and second antennal segment, fuscous third antennal segment with base narrowly pale, weak carina on lateral margins of pronotum, and structure of the male genitalia (Fig. 9). This species also has smaller dark spots located more anteriad on the vertex than in *G. litoralis,* and the collar possesses a large dark spot on either side of the middle.

Description of male. Length 5.39–7.00; general coloration pale grayish yellow, with brown to fuscous markings. **Head:** Width across eyes 0.76–0.80, vertex 0.28–0.36; frons either side of middle with longitudinal series of brownish-red to fuscous marks; vertex with two fuscous spots between eyes. **Antennae:** I, length 1.24–1.50, mostly fuscous with pale spots dorsally and a single pale stripe ventrally; II, length 2.62–3.18, brown or dark brown, sometimes slightly paler basally, but never distinctly bicolored; III–IV, fuscous, segment III narrowly pale basaly. **Labium:** Length 2.26–2.48; extending between metacoxae. **Pronotum:** Posterior width 1.09–1.20; disc lightly suffused with fuscous, especially posteriorly and around calli; calli sometimes with darker brown or brownish-red markings; collar with large dark spot either side of middle; lateral margins of disc with weak carina; posterior margin weakly convex overall, but with broad, shallow, concave region medially; mesoscutum with dark marks either side of middle and sometimes at lateral corners; scutellum marked with brownish red or fuscous either side of pale median stripe, and with two large fuscous marks laterally before apex. **Hemelytra:** Conspurcate, spots on clavus sometimes restricted to veins; apices of clavus and cuneus, posterior angles of corium, and inner margin of cuneus with slightly larger fuscous marks. **Legs:** Pale, with limited brown-

ish-red to fuscous markings mostly arranged in longitudinal lines; fore femora sometimes more extensively darkened; fore tibiae sometimes with two or three dark annuli; tarsi uniformly darkened. **Genitalia:** Figure 9.

Female. Brachypterous (forewings extending to abdominal segment V or VI), length 4.94–5.24, or macropterous, length 6.54; color and vestiture similar to male, except dorsum with fewer dark spots; eyes much smaller than in the male and with correspondingly broader vertex, width across eyes 0.76–0.85, width of vertex 0.40–0.44; length of antennal segment I 1.50–1.75, segment II 2.81–3.10; length of labium 2.52–2.66; posterior width of pronotum 0.88–1.10.

Etymology. From the Latin, *strigosus* (lean, thin), referring to the slender body form.

Distribution. Southeast Arizona and west Texas.

Holotype ♂. USA. **Texas.** *Jeff Davis Co.:* Fort Davis State Pk., 5,200 ft, Aug. 24, 1970, at lights, J. R. and M. H. Sweet (TA&M; deposited in the USNM).

Paratypes. USA. **Arizona.** *Cochise Co.:* 1♂, Douglas, Oct. 15, 1963, J. H. Russell (USNM); 1♂, SW Res. Stn., 5 mi W of Portal, 5,400 ft, Oct. 5, 1956, E. Ordway (AMNH). *Pima Co.:* 1♂, Molino Basin, Santa Catalina Mts., June 9, 1958, C. D. MacNeil (CAS); 1♂, 1♀, Mt. Lemmon, Santa Catalina Mts., Aug. 3–4, 1967, L. A. Kelton (CNC), 1♀, Santa Rita Mts., June 12, 1933, R. H. Beamer (KU); 1♀, Santa Rita Mts., 4,500 ft, June 27, 1928, A. A. Nichol (USNM); 1♂, 1♀, 6 mi N of Sonoita, May 19, 1989, swept from grasses, W. A. Jones (USNM); 3♂, 1♀, Tucson, Aug. 4, 1967, L. A. Kelton (CNC). *Santa Cruz Co.:* 1♂, 1♀, Mustang Mt., June 12, 1933, R. H. Beamer (KU); 1♀, Mustang Mt., June 12, 1933, P. Oman (USNM); 1♂, Patagonia, Sonoita Crk., Oct. 14, 1927, J. A. Kusche (CAS). **Texas.** *Jeff Davis Co.:* 4♂, same data as for holotype; 1♂, Fort Davis State Pk., Aug. 23, 1969, Board and Hafernik (TA&M).

Additional specimens. USA. **Texas.** 1♂, 226, P. R. Uhler collection (USNM). This specimen bears two Uhler identification labels for *Pallocoris suavis* Reuter, an externally similar species placed in the genus *Phytocoris* (*candidus* group) by Stonedahl (1988). One of these labels has "Tex." written in the lower left corner, which is the only locality data provided with the specimen.

Gracilimiris wheeleri, new species

Fig. 10

Diagnosis. Distinguished from *G. litoralis* and *G. strigosus* by its smaller size; shorter, uniformly pale first antennal segment; clavus and corium sometimes lightly suffused with fuscous, but without distinct dark spots; and male genitalia as in figure 10.

Description of male. Length 4.64–5.62; general coloration pale yellow or grayish yellow; head and pronotum more brownish yellow; pronotal disc usually lightly suffused with red. **Head:** Width across eyes 0.62–0.64, vertex 0.30–0.34; frons with obscure red markings either side of pale median line; vertex tinged with fuscous, especially bordering eyes, but without distinct dark spots. **Antennae:** I, length 0.98–1.15, pale brownish yellow; II, length 1.97–2.26, brownish yellow, sometimes darker brown near apex; III–IV, fuscous, segment III narrowly pale basally. **Labium:** Length 1.46–1.65; reaching between metacoxae. **Pronotum:** Posterior width 0.91–1.03; pos-

terior lobe of disc lightly suffused with fuscous, dark spots on posterior submargin sometimes faint or indistinct; collar and calli often with faint red or brownish-red markings; lateral margins of disc weakly carinate, posterior margin broadly convex with a weakly concave region medially; mesoscutum mostly fuscous; scutellum mostly fuscous dorsally, sometimes with narrow pale stripe medially, lateral margins broadly pale. **Hemelytra:** Pale gray or grayish yellow, usually with light to moderate suffusion of fuscous, especially along veins, inner margin of corium and on cuneus; postero-lateral region of corium and lateral margin of cuneus sometimes also lightly tinged with red; conspurcate pattern on membrane becoming noticeably denser distally. **Legs:** Pale brownish yellow with limited red or brownish-red markings, mostly restricted to ventral surface of femora and usually arranged in one or two longitudinal lines; tarsi usually slightly darker than tibiae. **Genitalia:** Figure 10.

Female. Submacropterous, with hemelytral membrane clearly shorter than in male, length 4.30–4.94; color and vestiture similar to male, except spots on hemelytral membrane usually restricted to region distad of areolar cells; eyes slightly smaller and vertex broader than in male; width of head across eyes 0.63–0.66, width of vertex 0.39–0.41; length of antennal segment I 1.20–1.35, segment II 2.23–2.41; length of labium 1.71–1.75; posterior width of pronotum 0.92–0.97.

Etymology. Named for our colleague and good friend Al Wheeler, Jr., who was the first collector to associate this species with its host plant, *Muhlenbergia porteri* Scribn.

Distribution. Southeast Arizona and west Texas.

Holotype ♂. USA. **Arizona.** *Graham Co.:* Pinaleno Mts., Stockton Pass, 5,200–5,500 ft, June 1–2, 1983, taken at mercury vapor light, R. T. Schuh and G. M. Stonedahl (AMNH).

Paratypes. USA. **Arizona.** *Cochise Co.:* 1♂, Chiricahua Mts., Cave Creek Ranch, Aug. 19, 1971, at light, K. Cooper (UCR); 1♂, Portal, 4,700 ft, Aug. 16, 1964, at light (UID); 1♂, Portal, 1,500 m, June 15, 1980, at UV light, R. T. Schuh and K. & R. Schmidt (AMNH). *Graham Co.:* 47♂, 3♀, same data as for holotype (AMNH). *Maricopa Co.:* 1♀, 7.5 mi SSE of Bumble Bee, 2,000 ft, Sept. 17, 1971, at light, M. A. Kolner and D. D. Covert (AMNH). *Pima Co.:* 1♂, Madera Cyn., Aug. 26, 1965, C. Slobodchikoff (UCB); 1♀, Sept. 4, 1955 and 4♂, 4♀, Sept. 23, 1955, Tucson, at light, F. G. Werner (UAZ); 8♂, 5♀, Sahuarita, Santa Rita Exp. Range, April 11, 1989, ex *Muhlenbergia porteri,* T. J. Henry and A. G. Wheeler, Jr. (PDA, USNM). **Texas.** *Presidio Co.:* 1♀, Presidio, July 30, 1968, at UV light, J. E. Hafernik (TA&M). *Randall Co.:* 1♀, Palo Duro Cyn. State Pk., Aug. 10, 1965, at light, J. C. Schaffner (TA&M).

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ANTITEUCHUS RUCKESI, A NEW DISCOCEPHALINE FROM PERU (HEMIPTERA: PENTATOMIDAE)

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Abstract.—A new species from Peru, *Antiteuchus ruckesi,* is described in the *incurvia* species-group of the nominate subgenus.

Ruckes (1964) proposed and characterized the *incurvia* species-group for 13 species in the nominate subgenus of the discocephaline genus *Antiteuchus* Dallas. Species subsequently added to this group are the 5 species described by Engleman (1976, 1983).

Many species of the *incurvia* group are known only from the holotypes or type series, and none is represented in collections by more than a few specimens. This paucity of specimens suggests that the group dwells in the forest canopy where it is relatively inaccessible to collectors. Specimens have come either from the vast basin drained by the Amazon River and its tributaries or from low lands of northern South America and Panama.

Most members of the *incurvia* species-group have a mesial process on the posterior margin of the last abdominal tergite of the male. The 3 species lacking this tergal process are *nebulosus* Ruckes, *grazia* Engleman and the species described here. The males of these species are separated by the following key:

1. Mediodorsal lobe of each paramere-head finely denticulate on superior part of posterior margin; second antennal segment about one-fourth length of third, all of last segment sordid ivory .... *graziae* Engleman
– Mediodorsal lobe of each paramere-head entire along superior part of posterior margin; second antennal segment about one-half length of third, last segment bicolored 2
2. Series of parallel carinae extending onto medioventral lobe of each paramere-head (Figs. 3, 4); axis of medioventral lobe and axis of paramere-shaft approximating right angle .... *ruckesi,* new species
– Series of parallel carinae not involving medioventral lobe of each paramere-head; medioventral lobe recurved, nearly paralleling axis of paramere shaft ...... *nebulosus* Ruckes

Antiteuchus ruckesi, new species
Figs. 1–6

Diagnosis. Last abdominal tergite lacking mesial process; medioventral process of each paramere-head bearing transverse carinae.

Description. Flavescent, mottled dorsally by retes and macules of dark punctures and infusions (Fig. 6).

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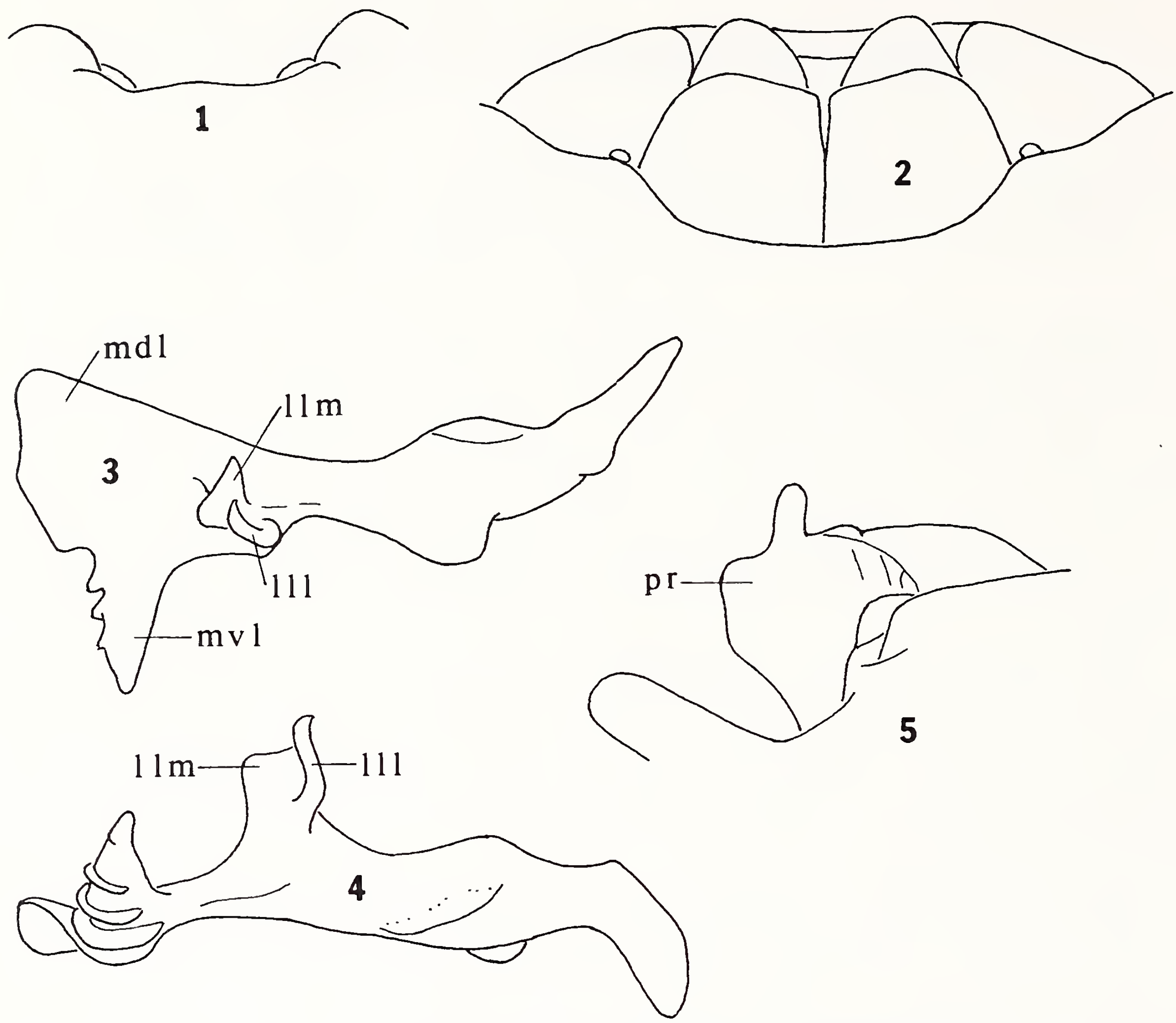

Figs. 1–5. *A. ruckesi,* new species. 1. Posterior margin of last abdominal tergite, dorsal view. 2. Genital plates. 3. Right paramere, lateral view. 4. Same, rotated 90°. 5. Proctiger, lateral view. lll, lateral lobe, lateral part; llm, lateral lobe, medial part; mdl, mediodorsal lobe; mvl, medioventral lobe; pr, proctiger.

Head. Lateral margins of head somewhat reflexed, moderately so along anteocular concavities; black edging of each jugum widening just before anteocular concavity into narrow border extending to eye. Vertex and postclypeus outlined in black, punctate lines, those on postclypeus continuing submarginally on anteclypeus, converging subapically. Punctures on disk of tylus black, those on juga dark castaneous.

First, second and basal 0.6 of third antennal segments dotted and streaked with fuscous; distal 0.4 of third segment, distal 0.7 of fourth, and distal 0.5 of last, excepting apical 0.1, fuscous; basal bands of fourth and fifth segments light stramineous to ivory, apex of fifth slightly darker. Setae on all segments much shorter than diameter of supporting segments.

Venter of head weakly, irregularly punctate. Apex of rostrum reaching onto third visible abdominal sternite.

Thorax. Anterolateral pronotal margins narrowly rimmed; collar poorly defined, obscure mesially. Fuscous suffusions connecting many punctures into lines and blotches forming four vague bands radiating from anterior to posterior pronotal margins.

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Fig. 6. Habitus.

Vague, mesial macule on basal disk of scutellum and even less well defined post-frenal macule resulting from networks of fuscous lines connecting punctures. Most punctures on coria similarly connected into lines and irregular macules; on each corium one diffuse macule mostly on endocorium between R + M vein and clavical suture; one more or less solid macule between R + M vein and post-frenal part of scutellum; and a small macule subapically on endocorium. Costal angle of each corium nearly reaching abdominal apex; margin joining membrane slightly sinuous. Membrane opaque excepting broad, fumose, apical border; veins simple, 6 or 7 in number.

Thoracic pleura rather uniformly punctate excepting impunctate evaporative areas; punctures moderately dense, black caudad of evaporative areas, castaneous elsewhere. Callus on each mesopleuron located on posterior margin submarginal to lateral margin; callus on each metapleuron in posterolateral angle but separated slightly from posterior margin; all calli ivory. Each ostiolar ruga extending about 0.4–0.5 distance from mesial limit of ostiole to lateral margin of metapleuron with a step down about

midway of ruga. Femora and sulcate surfaces of tibiae with many small, black spots; hind tibiae may bear a subbasal and a subapical annulus; tibiae and tarsi sometimes with rufous suffusion; setae on legs short, only some of those on tarsi longer than diameter of supporting segment.

Abdomen. Connexiva partially exposed; a large, black, triangular macule with apex mesad divided by each transverse connexival suture.

Density of punctation on sides of venter similar to thoracic punctation, but punctures weaker, becoming increasingly sparse toward meson. Spiracles black, ovoid. Lateral margins of venter narrowly black-bordered on both sides of incisures. Posterior margin of last tergite slightly trisinuate from dorsal view, without a mesial process (Fig. 1). Broad, shallow sulcus extending length of venter in females, as far as last sternite in males.

Genitalia. Basal plates subquadrangular, posterolateral angle of each broadly rounded, disk weakly convex (Fig. 2).

Lateral apical lobes of pygophore bending mesad apically, each about three times longer than its basal width, its mesial face flattened. Posterior pygophoral margin from caudal view moderately arcuate, with a dense fringe of setae on each side. Proctiger crested basally, bearing subapically a pair of erect, cylindrical, apically converging projections (Fig. 5). Parameres essentially 3-lobed; medioventral lobe concave laterally, acute apically, with 3 large laminae on mesial face, one small lamina dorsad of these and sometimes another ventrad of them (Figs. 3, 4); dorsomedial lobe convex laterally, narrowly rounded apically, without laminae; lateral lobe deeply bifurcate, mesial part flattened basally, lateral part subcylindrical, both parts curving dorsolaterad and acute apically.

Measurements (mm; both sexes). Head 3.3–3.5 wide across eyes, 2.3–2.5 long; interocular distance 1.90–2.05, between ocelli 0.90–1.05, across ocelli 1.20–1.30, from each ocellus to nearest eye 0.35–0.45. Length of segments 1–5 of antennae 0.85–0.95; 0.95–1.10; 2.05–2.30; 2.65–2.80; 2.70–2.80. Length of segments 1–4 of rostrum 1.1; 2.4–2.6; 1.4–1.6; 1.0–1.2. Pronotal width at humeri 6.8–7.3, length at meson 2.9–3.3. Width of scutellum at base 4.6–5.0, length 6.1–6.8. Body length excluding membranes 11.6–12.2.

Types. Holotype, male with pygophore on point and right paramere in microvial, labeled "PERU: Madre de Dios, Manu National Park; at uv light trap 15 Aug. 1980–30 Nov. 1981. Charles H. Hanson, cllr. Gift from The Burk Museum, mounted from alcohol 1986." Deposited in the California Academy of Sciences. Paratypes: 1 male, 2 females, all with same labeling as holotype. One female with abnormal left antennae of 4 segments, third segment 3.8 mm long, fourth 1.5 mm long and entirely ivory colored.

Etymology. The species described here is named for the late Herbert Ruckes in recognition of his pioneering work on the genus *Antiteuchus.*

ACKNOWLEDGMENT

The photograph (Fig. 6) was taken by Gerald Lenhard, Associate in the Department of Entomology.

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J. New York Entomol. Soc. 99(2):240–241, 1991

CONTEMPORARY RECORDS OF *BRACHYSTELES PARVICORNIS* (COSTA) IN THE UNITED STATES (HEMIPTERA: HETEROPTERA: ANTHOCORIDAE)

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Abstract.—The Palearctic anthocorid *Brachysteles parvicornis* (Costa) is reported from Maine and Massachusetts, together with host plant data and an illustration of the nymph.

The European anthocorid *Brachysteles parvicornis* (Costa) was recently reported from North America for the first time based upon several specimens collected in 1925 from Noodline, New Jersey, and Long Island, New York (Asquith and Lattin, 1990). We questioned whether this introduced species was established along the east coast and we did not expect the answer to appear so soon. It has. The senior author collected a series of specimens from two localities, one in Maine and the other in Massachusetts, in mid-September, 1990. Both locales were roadside sites.

A series of 13 females, 7 males, 2 V-instar, and 1 IV-instar nymphs was collected 5 mi E Bucksport, Maine, Hancock County, roadside, Hwy #1, 14 September 1990, ex *Picea glauca* (Moench) Voss. This site is on the central Maine coast. The second series, 4 females and 1 V-instar nymph, was taken at Roland C. Nickerson State Park, 3 mi W Orleans, Massachusetts, Barnstable County, roadside, Hwy 6A, 21 September 1990, ex *Pinus rigida* Mill. This site is on the north side of the base of Cape Cod. The spruce trees at the Maine site had lichen-encrusted branches, and the oribatid mite *Humerobates rostrolamellatus* Grandjean (family Ceratozetidae) was abundant on the branches. According to G. W. Krantz, Oregon State University (pers. comm.), this is a cosmopolitan arboreal mite that also is found in Europe. The branches of pitch pine at the Massachusetts locality showed few obvious lichens, but adults and tritonymphs of the same oribatid mite were also abundant. The presence of the mites supports the observations of Carayon (cited in Péricart, 1972) that the prey seem to be members of the mite suborder Oribatida.

The occurrence of mature nymphs, males, and females in early fall, combined with the earlier records of males and females collected in December (New York), and a male in May (New Jersey), suggests that adults of both sexes overwinter. Figure 1 shows the mature nymph.

This very small anthocorid (2.1–2.5 mm) could easily be overlooked among the debris beaten from coniferous trees. Almost certainly the species will be taken elsewhere along the eastern seaboard where it now seems to be well established.

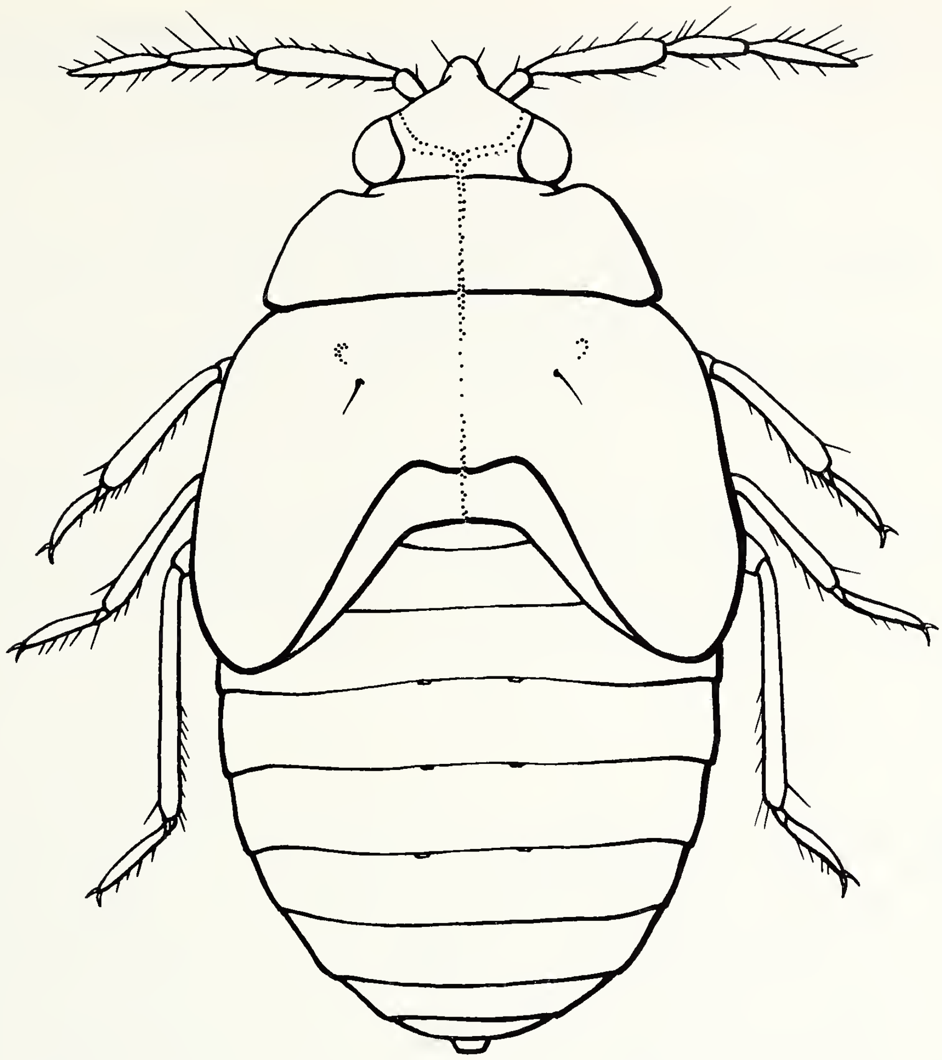

Fig. 1. Fifth-instar nymph of *Brachysteles parvicornis* from near Orleans, Massachusetts.

ACKNOWLEDGMENTS

Our thanks to G. W. Krantz and A. R. Moldenke for identification of the Acarina and B. B. Hall for the habitus drawing of the nymph. Support from the NSF, BSR-8514325, to J. D. Lattin is acknowledged.

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DESCRIPTIONS OF NYMPHS OF THE DELPHACID PLANTHOPPER *PISSONOTUS DELICATUS* (HOMOPTERA: FULGOROIDEA)

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Abstract.—First, third, fourth and fifth instar nymphs of *Pissonotus delicatus* Van Duzee collected from camphorweed (*Heterotheca subaxillaris* (Lam.) Britt. and Rusby: Asteraceae) in Florida are described and illustrated. Features useful in separating nymphal instars include differences in body size and proportions; spination of metatibiae, metatibial spurs, and metatarsomeres; and number of metatarsomeres and body pits.

Pissonotus delicatus Van Duzee is one of the most widely distributed of the 30 species of the North American planthopper genus *Pissonotus,* having been recorded from New York south to Florida and west to Utah, Texas, Oregon, and California (Beamer, 1952; Morgan and Beamer, 1949; Oman and O'Brien, pers. comm.). This delphacid has been collected on several composites: *Grindelia* sp. in Arizona (Morgan and Beamer, 1949), *G. squarrosa* (Pursh) Dunal. in Utah (Oman and O'Brien, pers. comm.), and *Haplopappus ciliatus* (Nutt.) DC in Kansas (Morgan and Beamer, 1949); the subspecies *P. d. melanurus* Van Duzee was collected on *G. camporum* Greene in California (Morgan and Beamer, 1949). Adults were described and male genitalia illustrated by Morgan and Beamer (1949) who noted considerable variability in the shapes and dentition of the aedeagal processes. This morphological variability and the different host affinities suggest that *P. delicatus* may represent a complex of sibling species. No other published information is available on the biology or immatures of this species.

This paper presents descriptions and illustrations of nymphs of *P. delicatus* collected on camphorweed, *Heterotheca subaxillaris* (Lam.) Britt. and Rusby (Asteraceae) in Florida.

DESCRIPTIONS

Specimens were preserved in 70% ethyl alcohol. The 5th instar is described in detail but only major differences are described for preceeding instars. Measurements are given in mm as mean ± SD. Length was measured from apex of vertex to terminus of abdomen, thoracic length along the midline from anterior margin of the pronotum to posterior margin of the metanotum, and width across the widest part of the body. One specimen of each nymphal instar was cleared in 6% KOH in order to examine distribution and number of body pits.

The collection data of specimens used for description are: FLORIDA: Broward Co., Fort Lauderdale, 11 September 1985, coll. P. Calvert. ex. camphorweed (8 adult

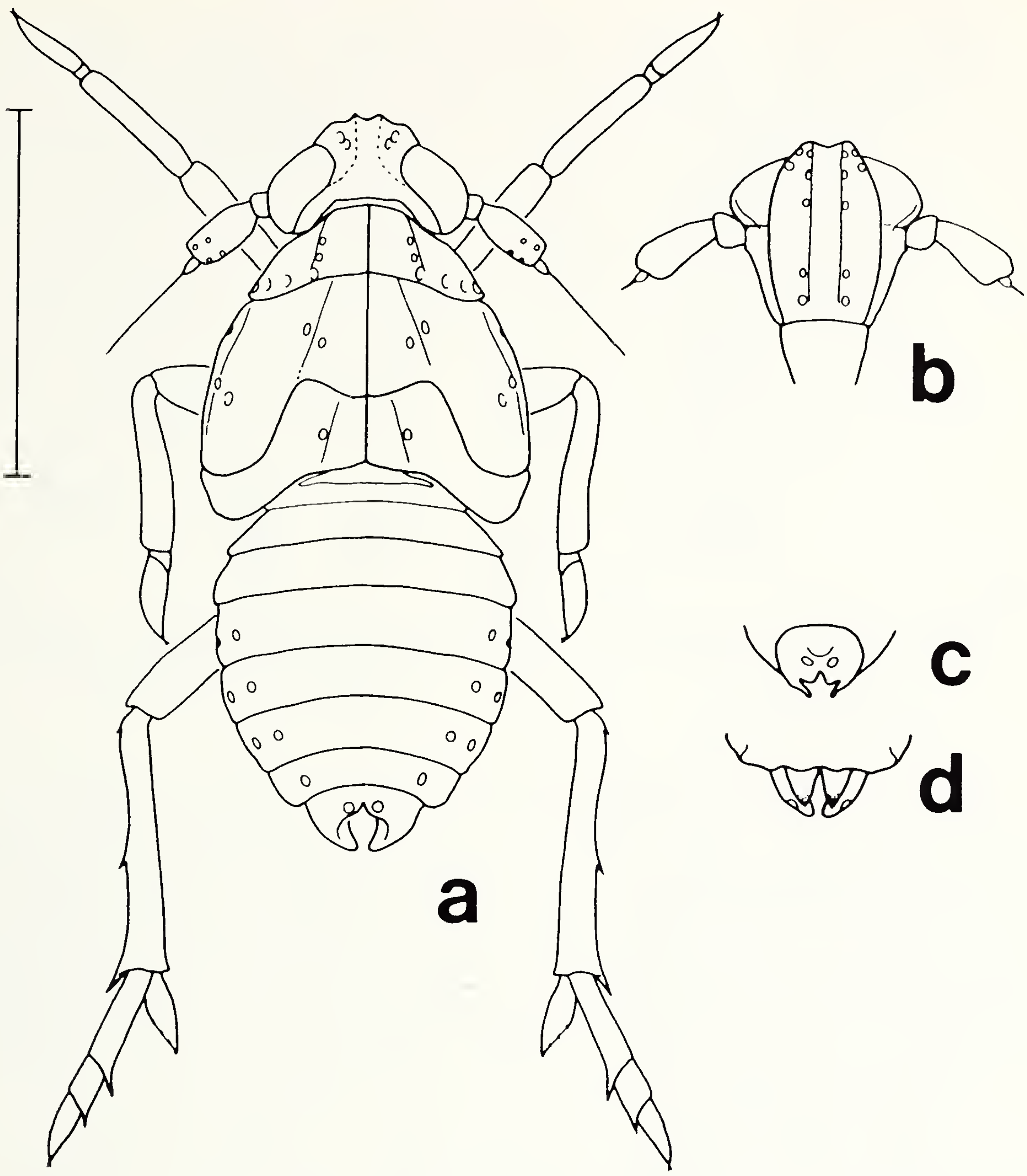

Fig. 1. *P. delicatus* fifth instar. A. Habitus. B. Frontal view of head. C. Ventral view of apex of abdomen of male. D. Ventral view of apex of abdomen of female. Bar = 1 mm.

males, 8 females; 10 fifth instar nymphs; 10 fourth instars, 8 third instars, 5 first instars). The male aedeagal process was identical to that of a Florida specimen illustrated by Morgan and Beamer (1949:fig. 24h). One third instar was stylopized, probably by a species of *Elenchus* (Strepsiptera: Elenchidae) (Borror et al., 1989; Kathirithamby, 1978).

Fifth instar (Figs. 1, 3D). Length 2.2 ± 0.33; thoracic length 0.7 ± 0.06; width 0.9 ± 0.09.

Form elongate, subcylindrical, slightly flattened dorsoventrally, widest across mesothoracic wingpads. Body whitish; anterior aspect of antennae and apices of pro- and mesotarsi brown (in alcohol).

Vertex quadrate, length subequal to width at base, posterior margin convex; carina on each side extending anteromedially from inner margin of compound eye and continuing onto frons as inner carina. Frons subrectangular; widest in middle, width

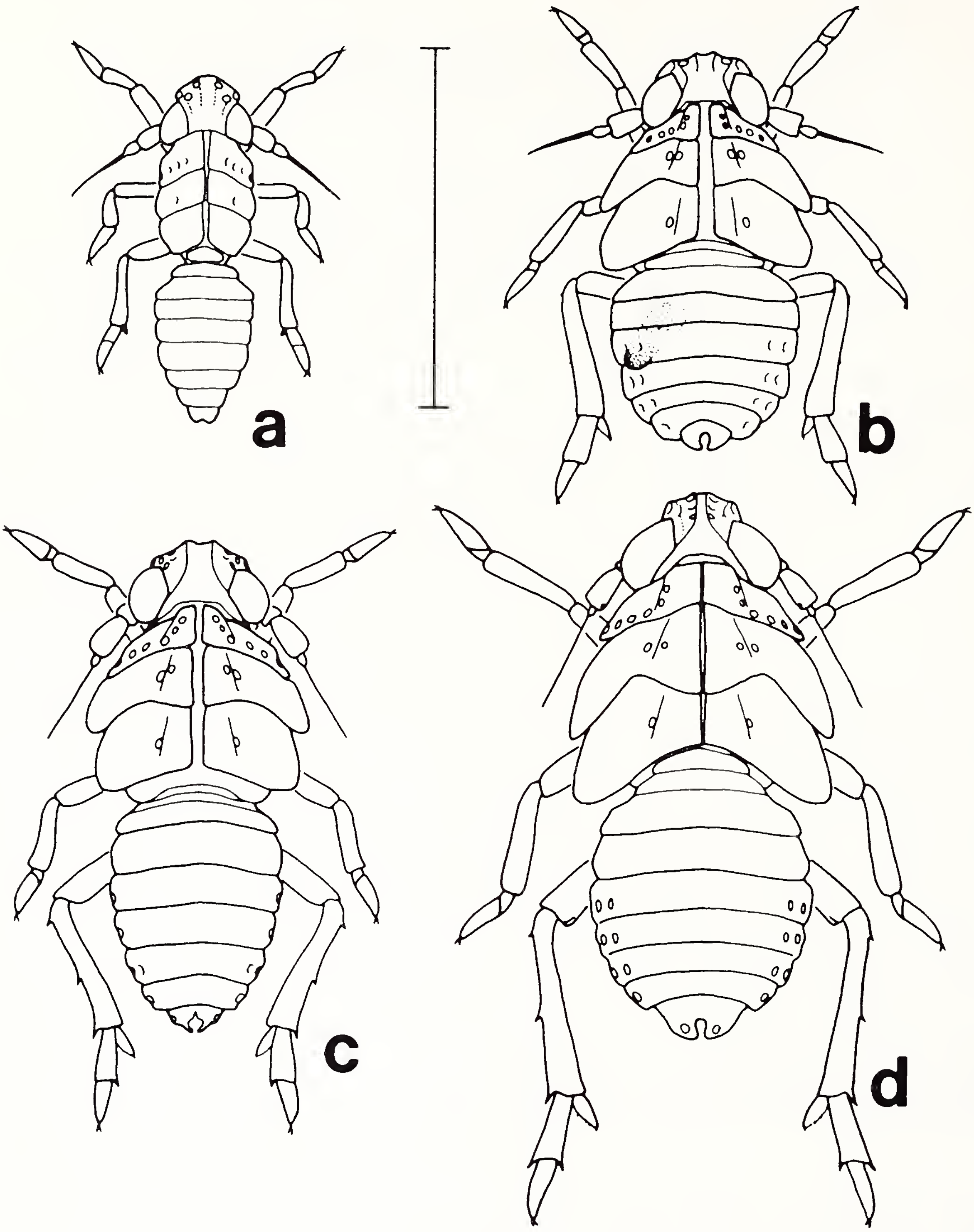

Fig. 2. *P. delicatus* nymphs. A. First instar. B. Stylopized third instar. C. Third instar. D. Fourth instar. Bar = 1 mm.

ca. 0.67× length; carinate lateral margins slightly convex, these outer carinae extending from vertex to near clypeal border and paralleled by pair of straighter inner carinae; 9 pits between each inner and outer carina (2 of these pits on dorsal aspect) and 4 pits between each outer carina and eye. Clypeus narrowing distally, consisting of subconical basal postclypeus and cylindrical distal anteclypeus. Beak extending to metatrochanters; 3-segmented, segment 1 obscured by anteclypeus, segment 2 slightly longer than 3; apex of segment 3 dark brown. Eyes red. Antennae 3-segmented; scape cylindrical, length subequal to width; pedicel subcylindrical, ca. 3× longer than wide

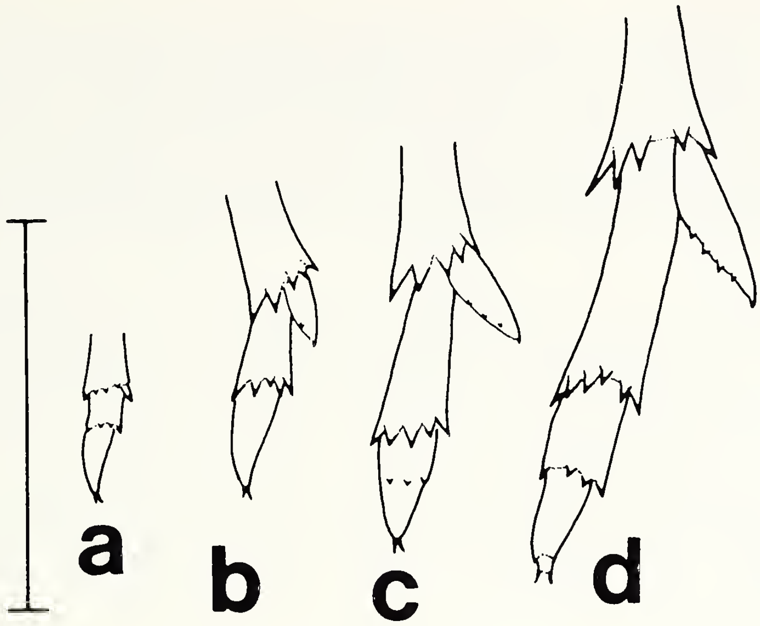

Fig. 3. *P. delicatus* apices of metathoracic legs, plantar surface. A. First instar. B. Third instar. C. Fourth instar. D. Fifth instar. Bar = 0.5 mm.

and ca. 3× length of scape, with 10–12 pitlike sensoria; flagellum bulbous basally, with elongate, bristle-like extension distally, bulbous base ca. 0.15× length of pedicel.

Thoracic nota divided by middorsal line into three pairs of plates. Pronotal plates subrectangular; anterior margin following posterior margin of head, posterior border sinuate; each plate with straight posterolaterally directed carina originating on anterior margin in median ⅓ and terminating in middle of plate, carina bordered along inner margin by row of 7 pits extending posterolaterally to lateral border of plate (lateralmost pits not visible in dorsal view). Mesonotal median length ca. 1.5–2× that of pronotum; each plate bearing an elongate lobate wingpad covering lateral half of metanotal wingpad; with posterolaterally directed carina originating on anterior margin in median ¼ and terminating on posterior margin; 2 pits, one on each side of carina and 3 pits in lateral ⅓. Metanotal median length ca. 0.5–0.75× that of mesonotum; each plate bearing an elongate lobate wingpad extending to tergite 3; with weak longitudinal carina originating on anterior margin in median ¼ and terminating near posterior margin; 1 pit just lateral to carina. Pro- and mesocoxae elongate, posteromedially directed; metacoxae fused to sternum. Metatrochanters subcylindrical, each with row of many minute teeth on posteromedial aspect which interlocks with those on the adjoining trochanter. Metatibia with 2 black-tipped spines on lateral aspect of shaft, an apical transverse row of 5 black-tipped spines on plantar surface and a subtriangular, flattened movable spur with row of 4–6 teeth on lateral aspect and 1 terminal tooth (Fig. 3D). Pro- and mesotarsi with 2 dark brown tarsomeres; tarsomere 1 wedge-shaped; tarsomere 2 subconical, curved, and with pair of apical claws and median membranous pulvillus. Metatarsi with 3 tarsomeres; tarsomere 1 cylindrical with apical transverse row of 5–7 black-tipped spines on plantar surface; tarsomere 2 cylindrical, ca. 0.25× length of tarsomere 1, with apical transverse row of 4 black-tipped spines on plantar surface; tarsomere 3 subconical, similar to terminal tarsomere of other legs.

Abdomen 9 segmented; slightly flattened dorsoventrally, widest across segments 4 and 5. Tergites 1 and 2 reduced; tergites 5–8 each with 3 pits on either side of midline (lateralmost pits not always visible in dorsal view). Segment 9 surrounding anus; with 3 pits on each side; female with 1 pair of subacute processes extending caudally from juncture of sternites 8 and 9; males lacking processes (Fig. 1C, D).

Fourth instar (Figs. 2D, 3C). Length 1.5 ± 0.05; thoracic length 0.6 ± 0.03; width 0.6 ± 0.02.

Antennal pedicel ca. 2× longer than wide and ca. 2× length of scape, with 6–8 pitlike sensoria; bulbous portion of flagellum ca. 0.25× length of pedicel.

Mesonotal wingpads shorter. Metatibial spur convex on both sides, with row of 1–3 teeth on lateral aspect and 1 terminal tooth. Metatarsi with 2 tarsomeres; tarsomere 1 with apical transverse row of 6 black-tipped spines on plantar surface; tarsomere 2 subconical, similar to terminal tarsomere of other legs, partially subdivided in middle, with transverse row of 3 very weak black-tipped spines in middle on plantar surface.

Abdominal subacute processes of female not apparent.

Third instar (Figs. 2B, C, 3B). Length 1.3 ± 0.05; thoracic length 0.5 ± 0.02; width 0.5 ± 0.01.

Antennal pedicel with 4 very weak pitlike sensoria; bulbous portion of flagellum ca. 0.33× length of pedicel.

Mesonotal median length slightly longer than those of pro- and metanota; wingpads weakly developed, covering metanotal wingpad laterally at base. Metatibial spur with 1 tooth on lateral aspect and 1 apical tooth. Metatarsomere 1 with apical transverse row of 5 black-tipped spines on plantar surface; tarsomere 2 lacking spines in middle. A stylopized third instar is illustrated in Figure 2B.

First instar (Figs. 2A, 3A). Length 0.9 ± 0.03; thoracic length 0.2 ± 0.02; width 0.2 ± 0.02.

Body pits very obscure.

Antenna with bulbous portion of flagellum ca. 0.5× length of pedicel.

Metatibia lacking lateral spines on shaft; apical transverse row of 4 black-tipped spines on plantar surface; spur weakly developed, slightly longer than longest tibial spine. Metatarsomere 1 with apical transverse row of 4 black-tipped spines on plantar surface.

ACKNOWLEDGMENTS

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MALES OF *TACHIONA DEPLANATA* SHARP AND *T. NITIDA* ASHE (COLEOPTERA: STAPHYLINIDAE) WITH NOTES ON THE HABITAT OF THESE SPECIES

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Abstract.—Males of *Tachiona deplanata* Sharp and *T. nitida* Ashe are described and illustrated. Specimens of *Tachiona* were collected from the inside of larval excavations of Hepialidae (Lepidoptera) in *Buddleja parviflora.*

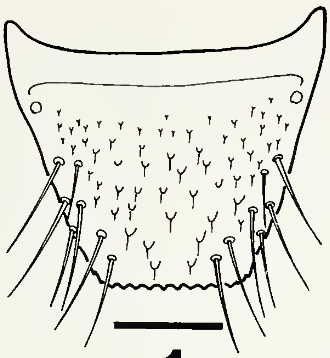
Four species of the unusual Central American staphylinid genus *Tachiona* Sharp have been described (Ashe and Wheeler, 1988; Ashe, in press). Two of these species are known only from females. *Tachiona deplanata* Sharp was known only from the original type series of three females. These were collected from Cordoba in the state of Veracruz, Mexico, and were described in the Biologia Centrali Americana (Sharp, 1883–1887). To my knowledge the species had not subsequently been collected until this past summer. *T. nitida* Ashe was described from a single female specimen collected in 1987 near Maltrata, at 1,900 meters, in the state of Veracruz, Mexico, by J. K. Liebherr and D. A. Millman (Ashe and Wheeler, 1988). Recently I collected 75 specimens, including males and females, of *T. deplanata* and a single male of *T. nitida* in the state of Veracruz, Mexico, 10.6 km W Mendoza, hwy 150, 1,860 meters, 18 July 1990. This collection provided the opportunity to describe and provide illustrations of the taxonomically important male characteristics and to briefly describe the habitat of these two species.

Males of *Tachiona deplanata* Sharp. Similar to females (see Ashe and Wheeler, 1988) with the following secondary sexual characteristics. Tergum VII without medial carina or longitudinal ridge. Tergum VIII produced posteriorly as a broad more or less truncate lobe, apical margin of lobe serrate (Fig. 1); surface of terga VII and VIII with numerous large, posteriorly directed asperities. Median lobe of aedeagus as in Figures 3, 4. Paramere as in Figure 2.

Males of *Tachiona nitida* Ashe. Similar to female (see Ashe and Wheeler, 1988) with the following secondary sexual characteristics. Tergum VII with small but distinct spinose carina on each side of midline and numerous scattered posteriorly directed asperities. Tergum VIII produced posteriorly as broad lobe, posterior margin of lobe deeply incised near each lateral border to produce a prominent spine on each side, medial portion of lobe broadly rounded and finely crenulate medially, surface

→

Figs. 1–4. *Tachiona deplanata* Sharp, male features. 1. Tergum VIII. 2. Paramere of aedeagus, external aspect. 3. Median lobe of aedeagus, lateral aspect. 4. Detail, apical lobe of aedeagus. Figs. 5–8. *Tachiona nitida* Ashe, male features. 5. Tergum VIII. 6. Paramere of aedeagus, external aspect. 7. Median lobe of aedeagus, lateral aspect. 8. Detail, apical lobe of aedeagus. (Scale line = 0.1 mm.)



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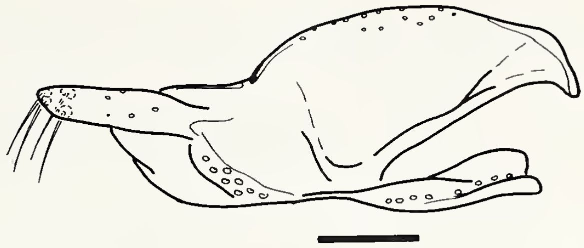

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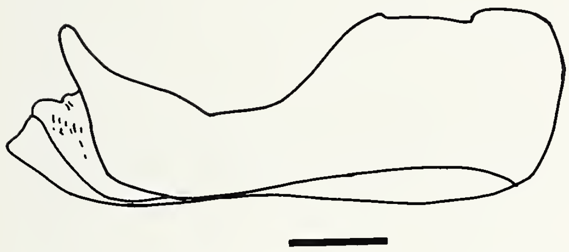

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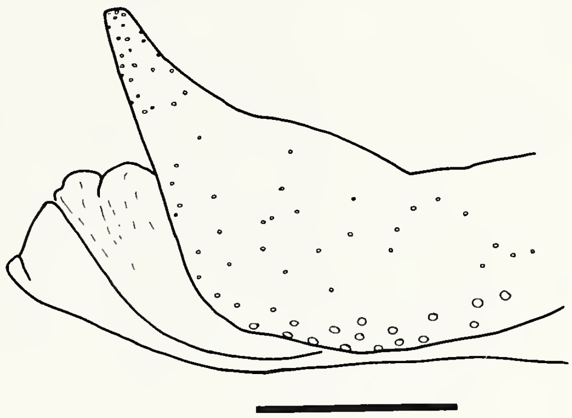

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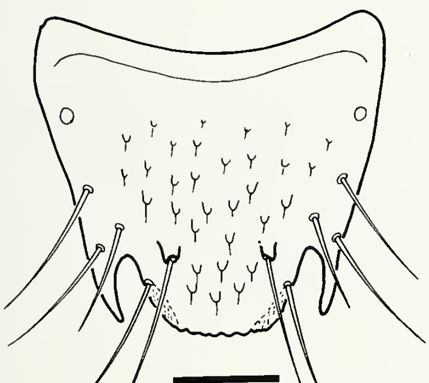

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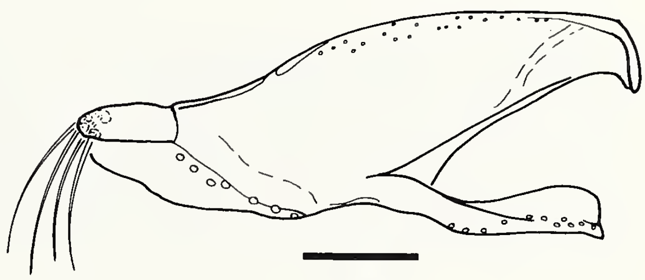

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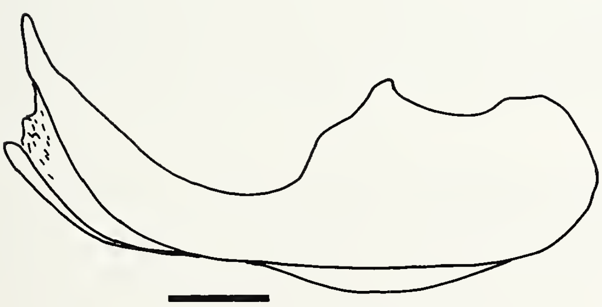

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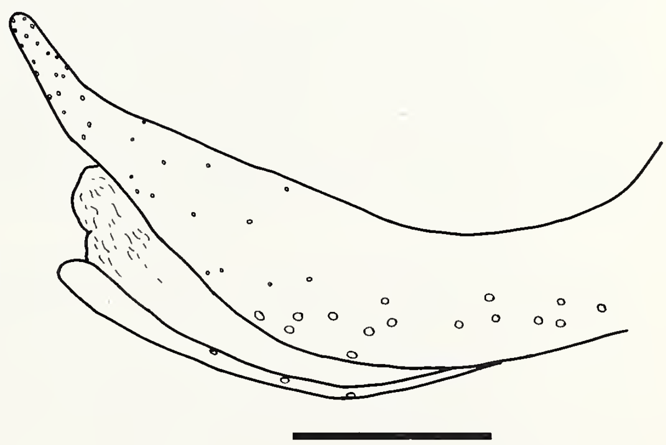

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of tergum with a low spine on each side of midline and numerous, posteriorly directed asperities (Fig. 5). Median lobe of aedeagus as in Figures 7, 8. Paramere as in Figure 6.

Habitat notes. The vegetation at 1,860 meters where these beetles were collected is primarily a somewhat xeric oak forest with a moderately dense understory of shrubs and small trees. A few pines are present, but these become more common at slightly higher elevations. All specimens of *Tachiona* were collected from the insides of webs covering hepialid moth burrows in *Buddleja parviflora* H.B.K. At this locality, *B. parviflora* is an abundant understory small tree. It is characterized by knarled or contorted multiple trunks, stringy bark, and silvery, opposite leaves. It is quite different in appearance from the smooth-barked *Trema* trees which served as the hosts of hepialid larvae in Costa Rica, the webs of which also contained numerous specimens of *Tachiona* (Ashe, in press). Hepialid burrows were abundant in trunks of *B. parviflora,* especially near the base of the tree. Specimens of *Tachiona* were found inside the webs of all burrows which contained an active hepialid larva. Webs covering burrows from which hepialids had emerged, even if very recently, did not contain either adults or larvae of *Tachiona.* At the date of this collection, most hepialids had already emerged, and consequently only about 1 in 10 of the webs contained *Tachiona. Tachiona deplanata* was by far the most abundant of the two species, and *Tachiona* larvae were associated with adults of this species in several webs. These larvae are very similar to those of *T. latipennis* Ashe and *T. nitida* described by Ashe and Wheeler (1988). The single *T. nitida* adult was collected from a web which also contained several adults of *T. deplanata.*

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THE BIOLOGY AND ZOOGEOGRAPHY OF THE LEGUME-FEEDING PATAGONIAN-FUEGIAN WHITE BUTTERFLY *TATOCHILA THEODICE* (LEPIDOPTERA: PIERIDAE)

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Abstract.—*Tatochila theodice* occurs in central Chile and (as three nominal subspecies) in Argentina from northwestern Patagonia to the Beagle Channel. It is unusual in its lineage in feeding on Leguminosae, including native species of *Vicia* and *Lathyrus* and probably introduced *Trifolium.* The early stages are so different from other known *Tatochila* that generic recognition may be warranted. The unusual distribution of the species can be understood in terms of glacial-interglacial vegetation dynamics in southern South America. The evolutionary basis for repeated switching from Cruciferous to Leguminous hosts in the Andean Pierini is not understood.

This is the eighth in a series of papers describing the life histories of the Pierini of the Andean region. Because of its alleged Holarctic derivation, this is an important group for reconstructing the historical biogeography of the Andean biota (Brown, 1987; Descimon, 1986; Shapiro, 1989, 1990a).

The largest pierine genus of the Andean region is *Tatochila* Butler, which was monographed by Herrera and Field (1959). They identified five species-groups, based on male genitalic characters and wing patterns. Group A consists only of *T. theodice* Boisduval and its two subspecies, *gymnodice* Staudinger from southern Patagonia and northern Fuegia and *staudingeri* Field from southern Fuegia. The form of the aedeagus in Group A is unique in the Andean Pierini. The wing pattern is complete and invariant in both sexes; the ventral hindwing vein-lines are narrow and sharply defined. Although *T. t. theodice* occurs in metropolitan Santiago, Chile it has not been previously reared and its biology has remained a mystery. Unlike other Chilean *Tatochila,* it is restricted to riparian corridors in the Andean and Coast Range foothills, has no consistent association with normal pierine hosts, and will not oviposit on these plants in captivity (Kellner and Shapiro, 1983). Shapiro (unpubl. data) had by 1988 failed consistently to obtain ova from all three Argentine subspecies, using conventional pierine hosts. In Tierra del Fuego, *T. t. staudingeri* was found commonly where no such plants occur.

In the austral spring of 1988 detailed observations of this species were made from northwestern Patagonia to the Beagle Channel, leading to the rearing of both northern and far-southern populations and the discovery that Herrera and Field's Group A is even more differentiated from the rest of *Tatochila* than had been suspected. Detailed documentation of the geographic range of *T. theodice* also led to the recognition of a pattern of probable importance for the interpretation of regional biota in a Quaternary framework.

Adult *T. theodice* from the northern part of its range in Argentina (Loncopué, Neuquén at least to Esquel, Chubut) are indistinguishable from Chilean material. The type locality of *theodice* is uncertain. No type specimen has been found and no neotype designated, but Herrera and Field (1959, pp. 477–478) restricted the type locality to "central Chile," apparently defined as from Los Andes (metropolitan Santiago) to Victoria, Malleco. The nominate subspecies thus occurs in two segments with almost no latitudinal overlap, separated by the high Andean crest.

The subspecies *gymnodice* was described from Punta Arenas, Magallanes, Chile; *staudingeri,* from Puerto Harberton in Argentine Tierra del Fuego. Herrera and Field had little material. Examination of over 100 Fuegian specimens reveals unambiguously that they intergrade completely. Although *gymnodice* is usual on the southern Patagonian mainland, I have not found any "pure" population of either subspecies in Fuegia. *Tatochila theodice* was the commonest butterfly near Río Grande, Argentine Tierra del Fuego in November 1988; both subspecies phenotypes and intermediates occur abundantly in a series of 56 ♂ 30 ♀ collected 25 November. In addition, the females are dimorphic (white and yellow), a previously unreported trait. Although this population cannot be characterized as one subspecies or the other, it is one of the southernmost known and offers a good comparison to the Chilean or northwestern Patagonian populations of nominate *theodice.* It will be referred to here simply as the "Fuegian population."

MATERIALS AND METHODS

On 13 November 1988 a female was taken flying near watercress at Junín de los Andes, Neuquén, northwest Argentine Patagonia. The following day a large colony was found on a boggy hillside seep near the shore of Lake Nahuel Huapí at San Carlos de Bariloche, Río Negro. Many males were seen patrolling, and three females observed near but not in patches of watercress. When no ovipositions had been seen in two hours, one of these females was collected. It and the Junín female were confined with watercress and dandelion flowers, both kept fresh with Water-Piks. By 20 November both females had died and a total of 18 eggs and one first-instar larva was found. The eggs had been laid on watercress, dandelions and the sides of the container. This was the first oviposition secured from this species in 11 years of trying. As the eggs hatched it became evident that the larvae would (and did) starve to death rather than eat watercress. Recalling the unexpected legume-feeding habit of *Tatochila distincta* Joergensen (Shapiro, 1986) and the abundance of naturalized white clover (*Trifolium repens* L.) at both the Junín and Bariloche sites, I added this plant and the surviving larvae accepted it at once. These larvae form the basis for the descriptions of the early stages of nominate *T. theodice* below; they were reared on *T. repens* under uncontrolled conditions in transit, ultimately eclosing in Davis.

Observations were made at Río Grande, Tierra del Fuego from 24–27 November 1988. The vegetation of the Río Grande site is described in Shapiro (1990b). Two Crucifers were present: *Thlaspi magellanicum* Comm. ex Poiret and *Draba magellanica* Lam. Neither was common; their combined biomass could not possibly support so dense a butterfly population. Fortunately, it was realized almost immediately that the host plants were two species of herbaceous vetches (Leguminosae), *Vicia bijuga* Gillies and *V. magellanica* Hooker, which trail on the ground and within

clumps of bunchgrass. They form an enormous biomass which, however, is inconspicuous when they are not in flower. Numerous ovipositions by at least six different females were observed over three days. Eggs are laid singly on leaves and stems with little consistency in position. Captive females oviposited on both vetches as well as the larger native Fuegian vetch *Lathyrus magellanicus* Lam., which was not present at this site. Larvae initiated feeding at once on all three plants, but rearing in transit was again on the readily available *Trifolium repens.* (This plant is naturalized in pastures in Fuegia from which the native vegetation is largely extirpated and also occurs in towns. *T. theodice* does not occur in its habitats.)

Six wild-collected Fuegian females were confined singly for 3–6 days with dandelions and various combinations of other common native plants from the Río Grande site, none of which elicited any ovipositions. The plants used were: Cruciferae: *Thlaspi magellanicum, Draba magellanica, Cardamine glacialis* (Forster) D.C.; Primulaceae: *Primula magellanica* Lehm.; Oxalidaceae: *Oxalis enneaphylla* Cav.; Compositae: *Perezia pilifera* (D. Don.) Hooker & Arn., *P. magellanica* Lag., *P. recurvata* (Vahl.) Less., *Hypochaeris incana* (Hooker & Arn.) Hoffman & Dusén, and *Senecio magellanicus* Hooker & Arn. Failure of these females to lay under identical conditions to those eliciting abundant oviposition on legumes was treated as significant.

Over 50 Río Grande larvae were reared, and matings and a second lab generation (on *T. repens* in Davis) secured. During a brief stay in Buenos Aires a number of Legumes and non-Leguminous weeds were collected from urban vacant lots and offered to second- and early third-instar Río Grande larvae which had been eating *Trifolium repens.* Cuttings were presented in groups of 2–3 species, always including one Legume; larvae had been starved for at least 3 hr. The plants used were: Leguminosae: *Vicia benghalensis* L., *V. angustifolia* L., *Medicago lupulina* L., *Medicago hispida* Gaert., *Medicago arabica* (L.) Huds., *Melilotus alba* Desr. ex Lam.; Cruciferae: *Sisymbrium officinale* (L.) Scop., *Brassica campestris* L., *Lepidium bonariense* L.; Polygonaceae: *Polygonum aviculare* L.; and Chenopodiaceae: *Atriplex hastata* L. (=*A. patula* var. *hastata*). No feeding was observed after 12 hr and the larvae were returned to *T. repens.* Descriptions of the Fuegian population are based on notes from life and preserved material of the first generation from Río Grande.

RESULTS

Behavior and ecology: T. t. theodice.—In northwestern Argentine Patagonia at the northern extreme of its range, the nominate subspecies is restricted to mesic habitats. It often occurs in creek bottoms fringed with willow, where it has a frequent (but misleading) association with introduced watercress, *Nasturtium officinale* R. Br. (Cruciferae). Males patrol along streamsides, often weaving in and out of willows. Both sexes visit flowers, particularly introduced dandelions (*Taraxacum officinale* L., Compositae). Both sexes may be found in *mallines* (wet meadows), but never on the intervening ridges in shrub-steppe. The distribution is thus discontinuous; since most *mallines* are used as pastures, most colonies occur on ranches. In the Lake District (Aluminé to Esquel) it becomes more generally distributed under more mesic climatic regimes, occurring in lawns and gardens in towns and along woods edges. Although there is a rich weedy and native Crucifer flora in this region, the only species whose ecological distribution resembles the butterfly's is watercress. *T. theodice* has never

been found associated with the native *Tropaeolum* (Tropaeolaceae), which are important pierine hosts.

Fuegian population.—At Río Grande this insect occurs in bunchgrass steppe. Adults fly in full sun only, with air temperature as low as 12°C and strong and turbulent winds. Activity was noted from about 1000 to 1745 hours. Both sexes thermoregulate in the same dorsal-basking attitude as *Parnassius* spp. (Papilionidae), with wings open flat at the sides and pulled down into a triangular configuration with the head at the apex. No other basking attitude was observed. Dandelion is visited frequently. Other flowers visited less often include the natives *Perezia* spp., *Primula magellanica,* and *Oxalis* spp.

Although *Hypsochila microdice* Blanchard was also abundant, virtually no interspecific interaction was seen with this similar-sized white butterfly. Male *T. theodice* patrol in a seemingly haphazard manner over the grass tussocks, frequently dipping to avoid the wind or to court a female. Courtships are very brief; copulation occurs within 15 sec if at all (8 observations). Males are easily lured to ground by pinched female decoys. Male-male chases are frequent and brief (20 sec). The flight of this species is much less direct and strong than that of *H. microdice.* It is much more likely to be picked up and carried away by the wind, and much more evenly distributed over the steppe than *H. microdice,* which is clumped in areas with more bare soil and relief (Shapiro, 1990b).

Life history: T. t. theodice.—All color names in quotation marks, and color numbers, refer to Kornerup and Wanscher (1978).

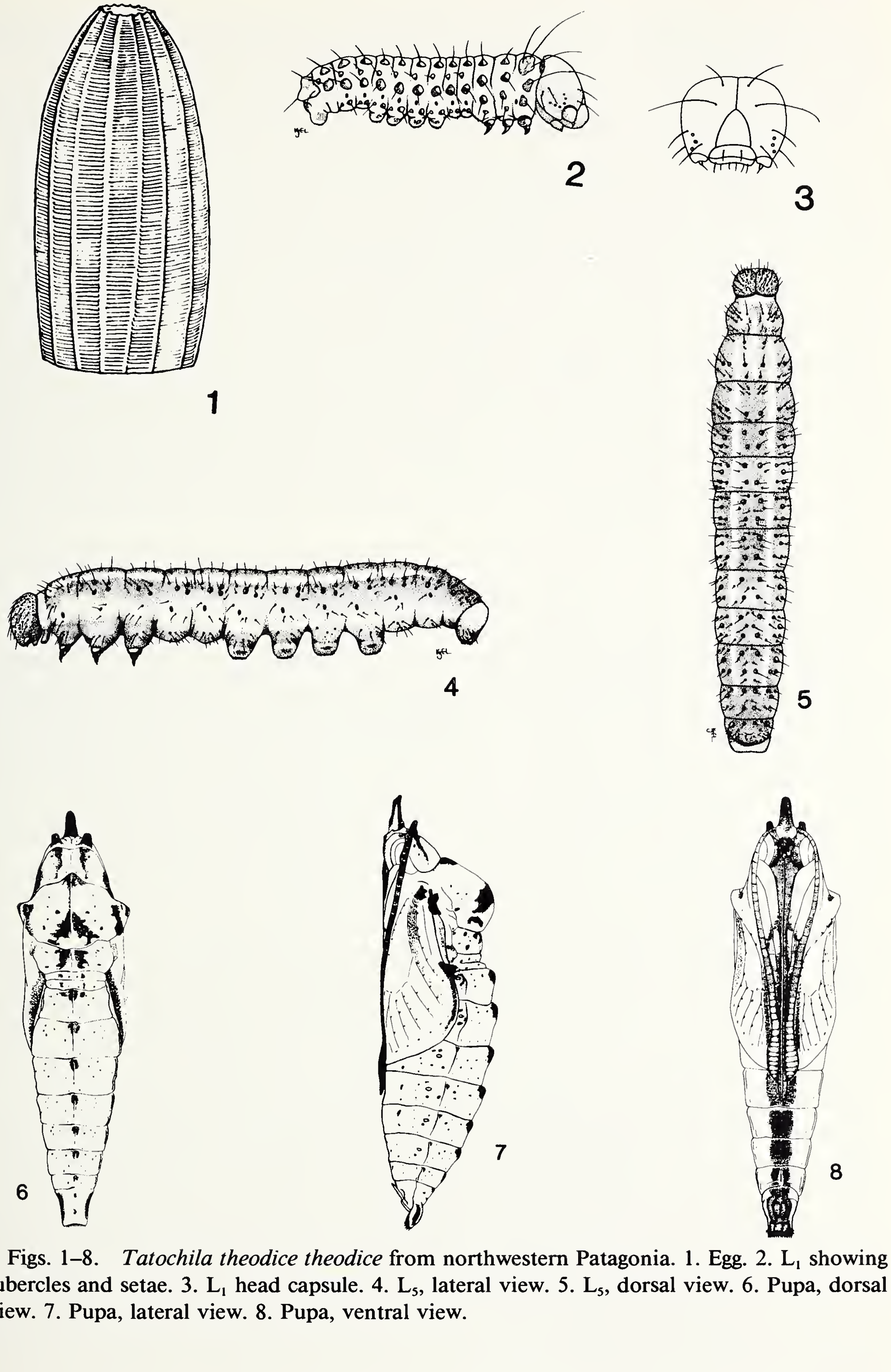
Egg (Fig. 1). Erect, fusiform but relatively broad, 0.88 × 0.35 mm. Chorion sculptured as illustrated, with about 13 vertical and numerous horizontal ribs; the vertical ribs forming a very distinctly beaded corona around the micropylar region. Light orange (6A6) when laid, turning slate gray ±10 hr before hatching. Laid singly in captivity and afield. The larva eats a hole below the top of the egg at hatch, but consumes little if any more of the chorion. Time to hatch, 5 days.

Larva: First instar (Figs. 2, 3). At hatch 0.97 mm. Light orange (6A6) with head apparently unmarked black; body darkening after feeding, becoming grayish. Tubercles in three sizes, black, bearing long primary setae. Feeds like a *Colias* larva, excavating strips between fine leaf veins, at rest on the midrib on the upper leaf surface between feeding bouts. Duration of instar, 2 days.

Second instar. After molt 1.9 mm long. Greenish gray (29D2), the usual *Tatochila* pattern of a dorsal median and subdorsal lines and a prothoracic collar, very pale yellow (5A5); tubercles black; head vaguely mottled dark brown and yellow. Habits as before. Duration of instar, 3 days.

Third instar. After molt 3 mm long. Slate gray ("greenish gray," 26C2), pattern as before, the dorsal line less distinct than the subdorsals. Head distinctly mottled with orange; ocelli and true legs black. Duration of instar, 5 days.

Fourth instar. After molt 7 mm long. Greenish gray (29D2); head black, mottled indistinctly with yellow ("absinthe yellow," 3C5), ocelli black; dorsal line faint, thin, whitish ("pale yellow," 3A3); subdorsal lines distinct, greenish yellow (3C5) tinged with orange ("dark orange," 5A8) to a variable degree, but especially on thorax and first two abdominal segments; a weak prothoracic collar, orange (5A8); area below the subdorsal lines gray (3D1) fading into dull yellow below the black spiracles, each segment containing an orange spot (sometimes two) within the yellow area; those on



Figs. 1–8. *Tatochila theodice theodice* from northwestern Patagonia. 1. Egg. 2. L_1 showing tubercles and setae. 3. L_1 head capsule. 4. L_5, lateral view. 5. L_5, dorsal view. 6. Pupa, dorsal view. 7. Pupa, lateral view. 8. Pupa, ventral view.

the thorax and first two abdominal segments usually strongest. Venter, including prolegs, dark slate gray (3E1); true legs black. Feeds openly on leaves, eating large holes. When disturbed, it drops from the plant. Duration of instar, 5 days.

Fifth instar (Figs. 4, 5). After molt 11.5 mm, reaching 29–31 mm. Pattern as before. Ground color dark ultramarine (20D7) with black tubercles bearing stiff black hairs, the tubercles smaller than usual for *Tatochila* but distributed as usual for the genus. Head pale bluish (23A3) mottled vaguely with orange and bearing black tubercles and ocelli. Mid-dorsal pale line bluish white, thin and not very distinct; subdorsal lines strong and contrasting, varying from bright orange-yellow ("orange," 5A7) to pale yellow (5A6); spiracles black; subspiracular area very pale bluish white (22A3), each segment containing two brick red (9B8) spots, strongly contrasting; intersegmental membranes conspicuously yellow; venter and legs variable, as in fourth instar or distinctly purplish or greenish. In color this is the most variable *Tatochila* yet observed, and the yellow-to-orange subdorsal stripes produce quite different visual effects (orange makes the ground color appear more purplish than it is). In captivity the larva eats entire rosettes of clover, resting on the exposed rhizome or on the cage when not feeding; it drops if disturbed and is very active in general for a *Tatochila.* Time to prepupation, 10 days.

Prepupa. Usually vertical, head up, attached as usual by the anal prolegs and a silken girdle. Color initially as in last instar but losing contrast, becoming indistinct grayish but with the tubercles more prominent than previously; future wing-case areas distinctly olive green. Time to pupation, 30 hr.

Pupa (Figs. 6–8). Length 21 mm; width at girdle 5.4 mm. Attached by the cremaster and girdle as usual. Ground color light blue gray ("bluish white," 23A2), tubercles black; dorsal midline with strong, black segmental keels; indistinct subdorsal lines, creamy white; top of head and eyes cream; legs, antennae and proboscis cases always chocolate brown (10F5); chocolate brown pattern otherwise extremely variable, from nearly absent to nearly covering the dorsum. Three prominences on head, mostly chocolate brown, the frontal prominence more than twice the length and width of the others and slightly curved dorsad. This is the strongest frontal prominence yet seen in *Tatochila*; it is reminiscent of the pupa of *Ascia.*

Eyes, wings and body pigmented in that order, white first appearing 40 hr and the black pattern roughly 24 hr before eclosion. Meconium bright red, as in other Andean Pierini (Shapiro, 1982). Time to eclosion (non-diapause), 17–20 days.

Fuegian population.—The life history of the Río Grande population is similar to that of northern *T. t. theodice.* All stages are smaller, but grow faster at the same temperatures. The following phenotypic differences were noted:

Egg. When laid, reddish orange (7A7) (slightly darker than *T. t. theodice*).

Larva: Fifth instar. Length at maturity 23 mm. Ground color dark bluish to violet gray ("dull violet," 18D4), the dorsal line white. Subdorsal lines broader than in nominate *theodice,* orange-yellow (4A8), as in the collar. Spiracles black; subspiracular area ice-gray (15B1), scarcely if at all yellowish, darker ventrad, with the usual orange spots; head mottled, bluish gray (20B3) and pale orange ("peach," 7A4), ocelli black; venter greenish gray (27B2), prolegs distinctly purplish ("lilac," 15B4); true legs black. Color more constant than in the nominate subspecies, but if anything even less typical for the genus.

Prepupa. As in *T. t. theodice,* but livid purple ("grayish magenta," 13B4)—exactly

the color of the prepupa of the North American Pierid *Euchloe hyantis* W. H. Edwards. This color change has not been seen previously in the Andean fauna.

Pupa. Smaller than *T. t. theodice* (18 × 4.5 mm), similar in form but the frontal prominence slightly less developed. Ground color initially purple (13B4) but turning fawn-buff (5A3) in about 40 min. Chocolate brown pattern highly variable as in the nominate subspecies. Facultative pupal diapause was observed, but the factors controlling it were not investigated. This population is bi-, perhaps partially trivoltine. Time to hatch (non-diapause), 13–17 days. Diapause pupae require at least 3 months of refrigeration at 2°C. In the lab-reared second generation, at L:D 14:10 hr, day/night temperatures 21°/10°C, the average development time, egg to adult, was 41 days.

Hybridization experiment. A reared Río Grande male was mated with a reared Junín-Bariloche female. Only 10 eggs were laid although the female lived for nearly a month; males were nearly constantly present but she never remated. Five of the eggs hatched and one larva pupated, but died without eclosing. Both the larva and pupa were larger even than nominate *theodice.* Since no difficulties were observed in rearing pure second-generation Río Grande animals eating the same food in the same growth chamber, genetic incompatibilities are suspected.

DISCUSSION

Taxonomic status.—Throughout its life history, *Tatochila theodice* displays apparently uniquely-derived attributes similar to those distinguishing genera in the Pieridae. The aedeagal morphology, used by Herrera and Field to distinguish their Group A, could indeed define a genus on its own, but these authors were quite conservative. Among traits which differentiate *theodice* from other *Tatochila* whose life histories are known are: the strong corona of the egg, apparently obligate use of Leguminous hosts, reduction of the larval tubercles, larval color scheme, very strong frontal prominence in the pupa, and drop-and-curl defensive behavior of the larva. However, I am refraining from naming a new genus to contain *T. theodice* until all of the "species-groups" of *Tatochila* have been reared and a phylogenetic analysis incorporating developmental characters has been completed.

The subspecific differences in the late larva, prepupa and pupa all suggest that Fuegian populations are derivative. The prepupal–early pupal color is an autapomorphy relative to the entire Andean Pierid fauna. The polarity of these morphoclines is of interest in interpreting the biogeographic history of *T. theodice.*

Quaternary migrations and contemporary distributions.—The distribution of this butterfly at first appears very strange. Although most of the historic references to it are Chilean, its distribution there is limited to a narrow latitudinal band (32°51′ to 38°15′S) around the edges of the Central Valley in a Mediterranean climate. Within this range there is no geographic variation in adult phenotype. In Argentina, where all the subspecies occur, its northernmost population is at Loncopué, Neuquén (38°04′S). There is thus hardly any latitudinal overlap, though it is possible that undetected populations exist especially on the Chilean side. Between the ranges, inhospitable Andean habitats intervene with elevations consistently over 2,000 m. The distribution of the species extends thence southward in the eastern foothills of the Andes all the way to Tierra del Fuego. *T. theodice* is absent from all of southern

(including archipelagic) Chile in these same latitudes, re-entering Chilean territory only in the steppe near Punta Arenas, and then from the east.

Caviedes (1990) has provided a paleoclimatic model consonant with the historical-biogeographic scenario advanced by Heusser (1981, 1983) and Caviedes and Iriarte (1989) for the evolution of the temperate biota of the Southern Cone in the Quaternary. This model fits the known distribution of *T. theodice* extremely well and renders it comprehensible. The present distribution of *T. theodice* strongly implies that it is intolerant of the very wet conditions prevailing today in austral latitudes west of the Andean crest. It is typical in Quaternary biogeographic reconstructions to assume little if any change in the climatic tolerances of species, i.e., climates change faster than adaptations do; otherwise it would be impossible to limit the number of hypotheses in the absence of fossil evidence.

In Caviedes' model, during Pleistocene glacial maxima pluvial conditions extended much farther north, and the high passes of the Cuyo district (Mendoza, San Juan), which are today unforested and summer-xeric, would have been forested, mesic, and potentially suitable for trans-Andean dispersal of *T. theodice* into its present Chilean range. Subsequently, mesic vegetation retreated drastically on both sides of the Andes and the Monte desert developed east of the crest, driving *T. theodice* south of the Cuyo into Neuquén. The passes in Neuquén, Río Negro and Chubut which are mesic today (and permeable to *theodice* northward but not in the south, where the Chilean side is too wet) were icebound in full-glacial time, and the lower Chilean altitudes somewhat wetter even than today. The confinement of *T. theodice* to the limited mesic ecotone between *Nothofagus* forest and the Patagonian steppe again suggests it would have been unable to occupy full-glacial southern Patagonia or Fuegia, whose climates were much harsher. Thus, both the entire Chilean range and the austral Argentine distribution of this butterfly are probably of Quaternary origin—the former full-glacial, the latter post-glacial.

The use of legumes.—The native host of *Tatochila theodice* in its northern range remains undetermined. There are several native Legumes in the region whose ecological and geographic distributions fit the butterfly's well; they include (in Chile) *Vicia vicina* Clos., *Lathyrus hookeri* D. Don., and *Astragalus berterianus* Reiche. In northern Patagonia the distribution of the butterfly closely parallels that of naturalized clover in *mallines,* but actual use in the field remains to be documented and no native candidate hosts have been identified. (The native Andean *Colias* are nearly all recorded only on introduced clovers and alfalfa, though ancestral use of *Lupinus* and *Astragalus* seems likely. Many of the Crucifer-feeding Pierini likewise are known only from naturalized European weeds (Kellner and Shapiro, 1983).)

The principal host associations of Pierini globally are Loranthaceae and the set of mustard-oil-producing families (Cruciferae, Capparidaceae, Resedaceae and the more distantly-related Tropaeolaceae) (Ehrlich and Raven, 1964). Cruciferae and Tropaeolaceae are widely distributed in the Andes. The former may have entered as recently as the Great American Interchange (3 MYA), but the latter are autochthonous. Legumes are ancient, ancestral hosts of two other Pierid groups, the Coliadinae and Dismorphiinae, but except for the genus *Colias* and the Palearctic *Leptidea,* these animals feed not on Papilionaceae but on Mimosoid and Caesalpinoid Legumes. The scattershot occurrence of Legume-feeding in *Tatochila* and *Hypsochila* (Shapiro, 1986, 1990a, b) suggests it is a derivative condition which has arisen several times

in the Andean Pierini. All the native hosts (*Astragalus, Vicia, Lathyrus*) are, moreover, advanced Papilionaceae which probably entered South America in the Great American Interchange (Raven and Axelrod, 1974). *Colias* is probably also only of Quaternary vintage in the Andes (Descimon, 1986; Shapiro, 1990a). *Tatochila* and its relatives have traditionally been considered Quaternary derivatives from the Holarctic as well (Dixey, 1894; Elwes, 1894; Grote, 1900), but this scenario is increasingly untenable (Shapiro, 1990a).

"Convergent or parallel evolutionary change repeated across diverse taxa and accompanied by evidence of similarity of selective forces is unlikely to occur by chance alone" (Pagel and Harvey, 1988). Are there obvious ecological "selective forces" favoring a repeated shift from mustard oil plants to Papilionaceous Legumes in the Andean-Patagonian fauna? In Fuegia, the biomass of native Legumes in *Tatochila-Hypsochila* habitats far exceeds that of Crucifers and allows the maintenance of very dense populations and the occupation of communities otherwise closed to Pierini. However, in the case of *Tatochila theodice,* as noted above, occupation of the far south is probably a recent development, while Legume-feeding must have evolved farther north.

Cases of parallel host-switching suggest the existence of chemical "bridges" among the plant taxa (Ehrlich and Raven, 1964; Ehrlich and Murphy, 1988). If there are such bridges between the Cruciferae and the Papilionaceous Legumes, it is odd that they have not been crossed in the Northern Hemisphere, where appropriate Pierini and all the plant genera concerned are well represented. On the other hand, the apparent unacceptability of the various Legumes, including *Vicia* spp., from Buenos Aires to *Tatochila theodice* suggests that the far-southern vetches may be chemically "special." The one obvious chemical trait they display is indigo production (Shapiro, unpubl.), but this is not a Crucifer trait. The basis for Legume-feeding by *Tatochila* is a mystery.

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DESCRIPTION OF MATURE LARVA AND NESTING BEHAVIOR OF *PSEUDOSCOLIA MARTINEZI* SUÁREZ (HYMENOPTERA: SPHECIDAE)

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Abstract.—The mature larva of *Pseudoscolia martinezi* Suárez, 1981, is described, and details are offered on adult nesting behavior. The main morphological characters of the larva are mandibles tridentate, well-developed galeae, spinnerets bigger than labial palpi, and the appearance of the epipharynx, which is similar to that of the known larvae of the Cercerini. The females of this species nest in small aggregations of 5–10 individuals, leveling the mound during the excavation of nests. They show variability in the practice of temporary closures, with some females leaving the nest open while others close the burrow during provisioning. Adult females capture Halictidae as prey.

The subfamily Philanthinae includes more than 1,000 species distributed among 11 genera (Bohart and Menke, 1976), making it one of the most important subfamilies within the Sphecidae. Most studies on the biology and preimaginal stages of the Philanthinae deal with species of *Philanthus* and *Cerceris,* two genera which are extensively distributed. Data on the biology and preimaginal stages of other genera are scanty but valuable, because in some cases their systematic position is not well established. Such is the case with *Eremiasphecium* Kohl, *Philanthinus* Beaumont, *Listropygia* Bohart, *Odontosphex* Arnold, and the genus dealt with here: *Pseudoscolia* Radozskowski.

Twenty species of *Pseudoscolia* are now known, eighteen of which range from northwestern Africa to southwestern USSR. Of the two remaining species, one is found in Mongolia and the other in arid areas in the southeast Iberian Peninsula (*P. martinezi*). In general, the species of *Pseudoscolia* have a very restricted distribution, occupying desert areas of the Palearctic Region, where they constitute typical elements of the eremic fauna.

Very little has been published on the biology of *Pseudoscolia.* The only sound information was offered by Beaumont (1949), concerning a male of *Halictus* Latreille (Apoidea: Halictidae) as the prey of *Pseudoscolia tricolor* (Giner Marí).

In this article, the mature larva as well as several aspects of the nesting behavior of *Pseudoscolia martinezi* are described. Observations were conducted from 18–25 June, 1989 in the Rambla of Tabernas, Almeria, Spain.

DESCRIPTION OF MATURE LARVA

The description of the larva is based on two specimens. The following abbreviations are employed in the description: d = diameter, h = height, l = length, w = width.

General appearance

Small fusiform body (l = 7 mm, w = 2.1 mm). Pleural lobes well-developed. Posterior end protuberant, the anal lobes forming a tubular projection on which the anus is located apically (Fig. 2). Anal lobes similar in size, the subanal being slightly bigger.

Whole surface of integument spinulose, the spinules (l = 5–10 μm) being more numerous toward the anterior end of the body. Scattered setae (l = 20 μm), more numerous in the posterior end.

Prothoracic spiracles (d = 75 μm) slightly bigger than the rest (d = 60–65 μm). Walls of atrium lined with lengthened irregular polygons (Fig. 1); opening to subatrium unarmed.

Whitish coloration, the spiracles appearing slightly brownish; mandibles, maxillary and labial palpi, galeae and antennae also of this brown color.

Head

Slightly higher than wide (h = 0.79 mm, w = 0.76 mm) (Fig. 3). Antennal orbits circular (d = 55 μm), inconspicuous; antennae moderately long (l = 39 μm, maximum d = 19 μm). Coronal suture well-developed (l = 0.24 mm); parietal bands absent.

Head capsule with scattered punctures, which are denser on the clypeus; small setae emerge from some of these punctures.

Mouthparts

Labrum (w = 0.34 mm) with even anterior edge, and with a faint notch in the center (Fig. 4a); some setae appear on the apical third and several sensilla on margin. Epipharynx spinulose on the anterior edge, lateral margins and basal area, a naked area appearing on the medial part (Fig. 4b). Sensory areas with 6 pores (d = 5 μm) on each side; some sensillae also appear on the central part of the anterior edge.

Mandibles thin (w = 0.195 mm, l = 0.37 mm) with three teeth on the internal margin and with a seta at the base (Fig. 3).

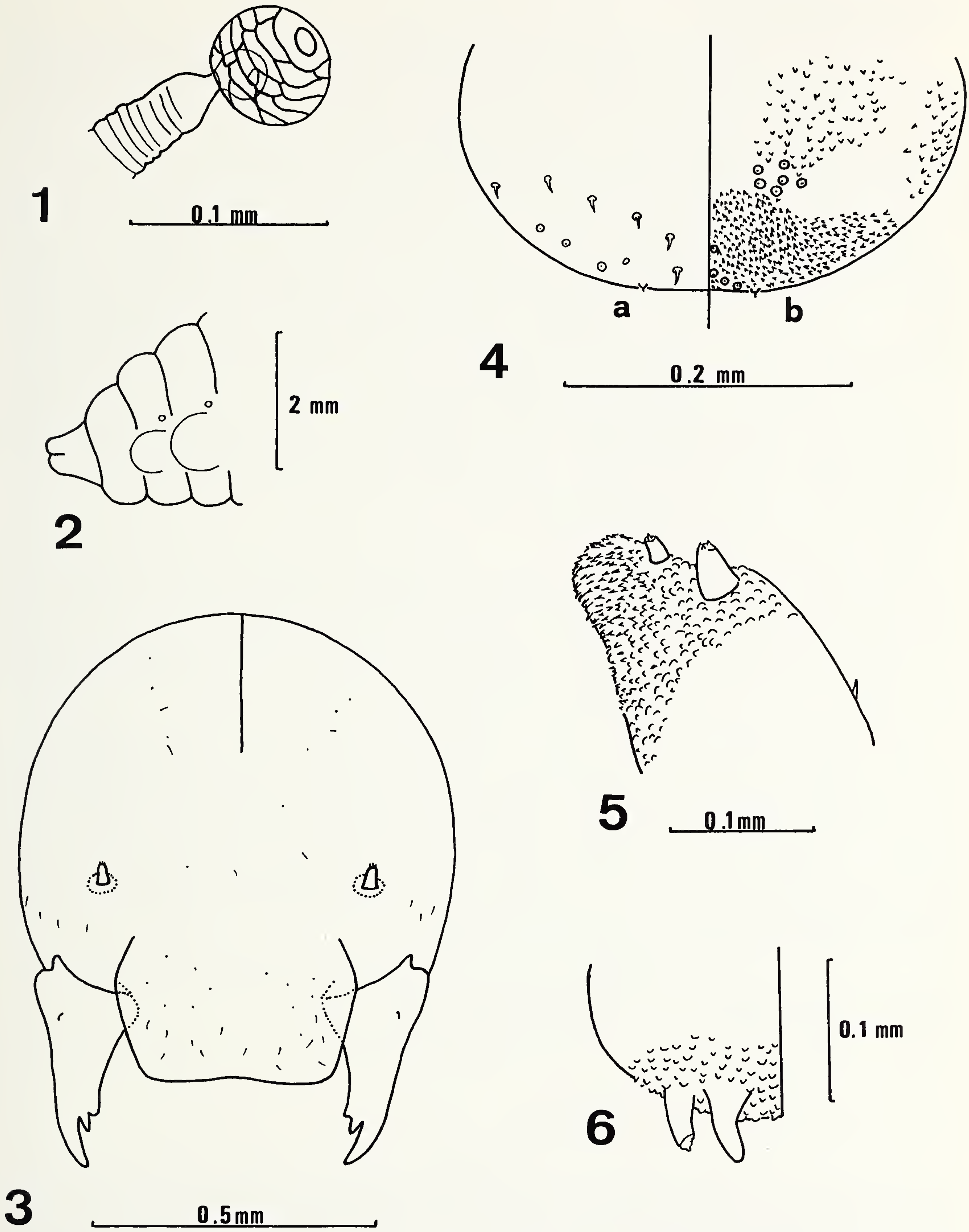
Maxillae, as in the other Philanthinae, projecting as large, free lobes. Lacinial area spinulose (Fig. 5), some setae appearing on ventral face. Maxillary palpi (l = 45 μm, d = 25 μm) much bigger than galeae (l = 20 μm, d = 12 μm), which are very thin.

Labial palpi (l = 45 μm, d = 25 μm) smaller than the spinnerets (l = 55 μm, d = 15 μm), which clearly exceed them (Fig. 6).

NESTING BEHAVIOR

Nesting area

The studies on nesting behavior were carried out in the Rambla de Tabernas, on the road that goes through the western spurs of the sierra of Alhamilla. The area belongs to the Almeriense sector, of the Murciano-Almeriense province of the Mediterranean region. It has an approximate altitude of 275 m, and the annual precipitation is lower than 300 mm.



Figs. 1–6. Mature larva of *Pseudoscolia martinezi* Suárez, 1981. 1. Spiracle (atrium and subatrium). 2. Last four segments of the abdomen (lateral view). 3. Head (frontal view). 4a. Labrum. 4b. Epipharynx. 5. Right maxilla (dorsal view). 6. Labium (oral surface, right half).

Nesting behavior

The females nested in small aggregations with from five to 10 individuals occupying areas of about two square meters, although some females established their nests in isolation. Nests were located in horizontal sandy areas, with sparse vegetation, although the entrances of some nests were placed near small plants.

The females became active at about 0930, becoming much less active from 1500 onward. They spent the night inside the nests, closing them from inside.

Females used their forelegs to throw sand backwards under the body. Periodically, the female went outside to remove the accumulated sand from the burrow, and this sand was scattered in such a way that it did not accumulate near the entrance. The female moved backwards to level the ground, with her head towards the entrance, about 6 cm away from the opening of the nest, and returned to the entrance while raking sand. The operation was repeated several times before the female reentered the nest and continued excavation of the main burrow, only raking sand when going to the entrance. Burrows showed a slight slope at the beginning, but after 6–8 cm they sloped strongly downward at an angle of 55–65° until a depth of 20–25 cm was reached, where the cells were located.

With respect to temporary closures, five females left the nest open during provisioning, while the other two made temporary closures. If the entrance remained open during provisioning trips, the wasp entered directly into the nest with her prey. If there was a temporary closure, the wasp opened and entered the nest, releasing the prey inside near the entrance. Immediately, she then turned around, seized the prey by its antennae with her mandibles and dragged it into the burrow.

Four nests were excavated. Three of them had a closed cell with the larva in different stages of development, while the other one only had some prey. In two of the three nests in which a larva was found, some prey were also found stored in the main burrow, which indicates that the nests are multicellular. Because this species seems to reach its peak activity (at least in the area studied) towards the end of June and the beginning of July, the excavated nests were probably recently dug, which would explain their relatively simple structure.

Ten prey were taken from nests, all of them bees belonging to the family Halictidae:

—*Halictus* (*Vestitohalictus*) *vestitus* Lepeletier: 1♂.
—*Lasioglossum* (*Evylaeus*) *immunitum* (Vachal): 1♂.
—*Lasioglossum* (*Evylaeus*) *planulum* (Pérez): 2♀♀.
—*Nomiodes minutissima* (Rossi): 4♀♀.
—*Nomiodes variegata* (Olivier): 2♀♀.

Prey may have been captured on plants, since it was common to see females fly over the bases of *Salsola webbii* (Moq. 1840) (Chenopodiaceae). The females seemed to show a preference for this plant, and in fact, when Suárez (1981) described the species, he commented on the fact that most of the specimens appeared at *Salsola* sp. and did not visit other species in the same area.

Natural enemies

In the nesting area several females of *Pterella melanura* (Meigen) (Diptera: Sarcophagidae) perched on little stones and branches and pursued prey-laden females.

These miltogrammine flies are possibly cleptoparasites of *Pseudoscolia martinezi,* although no *Pterella melanura* larvae were found in the nests.

DISCUSSION

The larvae of Philanthinae were characterized by Evans (1957, 1959) on the basis of a reduction in the size of the galeae, an increase in the number of spinules of the tegument, slender mandibles and a tubular-shaped anal segment. All these characters appear in the larva of *Pseudoscolia martinezi,* which, however, shows certain unique characters among the Philanthinae: the very small notched shape of the labrum and walls of spiracular atrium with lengthened polygons.

Both the tridentate mandibles, a character that *P. martinezi* shares with the larvae of *Philanthus,* and the very conspicuous galeae, shared with those of Cercerini, were considered as primitive by Evans (1959, 1964). However, *P. martinezi* has well developed spinnerets, which are longer than the labial palpi. This trend towards a greater development of the spinnerets was pointed out by Evans (1964) as a specialized character, and is shared by *P. martinezi* and by the Cercerini. Also, the epipharynx of *P. martinezi,* with a considerable area medio-basally devoid of spinules or papillae, is similar to that appearing in Cercerini (in *Philanthus* and Aphilanthopsini most of the surface of the epipharynx is spinulose). The fact that a specialized character, such as the strong development of the spinnerets, is shared by *P. martinezi* and the Cercerini accords with the opinion of Bohart and Menke (1976), based on the morphology of the adults, that the Cercerini and *Pseudoscolia* evolved from a common ancestor.

The leveling of soil during excavation of the nest seems, for the moment, to be the only specialized trait observed in the nesting behavior of *P. martinezi.* Like *P. tricolor* and many other Philanthini, they capture bees as prey, whose use seems to be ancestral in the Philanthinae. Most of the females of *P. martinezi* left the nest open during provisioning, although some cases were observed in which temporary closures were made. Although this behavioral trait is sometimes characteristic of each species, cases have been observed in which the occurrence of temporary closures varies, even among individuals within the same aggregation (Evans, 1966; Evans and O'Neill, 1988; Kurczewski, 1969, 1982; O'Neill, 1990). The intra-populational variation observed suggests that this trait is of no value for establishing relations with other genera.

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A NEW SPECIES OF *CALATHOTARSUS* (ARANEAE: MIGIDAE) FROM CHILE

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Abstract.—*Calathotarsus pihuychen,* a new species from San Antonio Province, Región de Valparaíso (V), Chile, is described and illustrated. Its burrows are described and compared with the burrows of other Chilean Migoidea.

The genus *Calathotarsus* contains two described species, *Calathotarsus coronatus* Simon (1903) from Chile (type species of the genus) and *C. simoni* Schiapelli and Gerschman (1975) from Argentina. Like other Migidae, these spiders close the entrance of their burrow with a trapdoor (Claude-Joseph, 1926, 1930; Schiapelli and Gerschman, 1975). During a recent collecting trip to Chile a new species of *Calathotarsus* was collected. The burrows of this new species were observed and compared with those of the other Chilean trapdoor spiders. Interestingly, the structure of the burrows varies widely, and it is very easy to distinguish the burrows of the four different trapdoor species collected in central Chile. A similar situation was found by Goloboff (1987) for the trapdoor genera in northwestern Argentina.

MATERIALS AND METHODS

Abbreviations used in this study are standard for the Araneae. All measurements are in millimeters.

Leg spines and claw teeth are noted as in Goloboff and Platnick (1987). All specimens are deposited in the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires.

FAMILY MIGIDAE SIMON

The family Migidae has been traditionally defined by three synapomorphies: cheliceral rastellum absent, thoracic fovea recurved, and cheliceral fangs with lateral keels (Raven, 1985). Goloboff and Platnick (1987) mentioned a fourth synapomorphy of the group: the absence of spigots on the basal article of the PLS. An additional character that seems to support the hypothesis of migid monophyly is the transformation of the spines of leg III (and to a lesser extent those of leg IV) into weaker spiniform setae (Fig. 3). This condition has been mentioned or illustrated in descriptions of migid species (see Legendre and Calderón, 1984; Goloboff and Platnick, 1987; Griswold, 1987a, figs. 14–16, 86, 213, 1987b, figs. 24, 25, 56; Dresco and Canard, 1975, fig. 2), but has not been stressed as a unique character. The successive sister groups of Migidae, the families Actinopodidae, Ctenizidae (Raven, 1985, fig. 256), Idiopidae (Platnick and Shadab, 1976, figs. 9, 11), Cyrtaucheniidae, and Atypoidina and Tuberculotae (except some Theraphosoidina) have numerous and strong

spines on the patella, tibia and metatarsus III. Although some Theraphosoidina (Raven, 1985:37, 1987) have posterior legs with weak or absent spines, the plesiomorphic state for Tuberculotae is clearly the presence of strong (and elongated) spines on the posterior legs (because they are present in the successive sister groups of Theraphosoidina: Nemesiidae, Dipluridae, Hexathelidae, and Mecicobothrioidina).

Calathotarsus pihuychen, new species
Figs. 1–10

Type.—Female holotype (with burrow), Quebrada Córdoba, 5 km E El Tabo, Prov. de San Antonio, Región de Valparaiso (V), Chile, Goloboff, Maury, Szumik coll., Nov. 1988, deposited in the Museo Argentino de Ciencias Naturales.

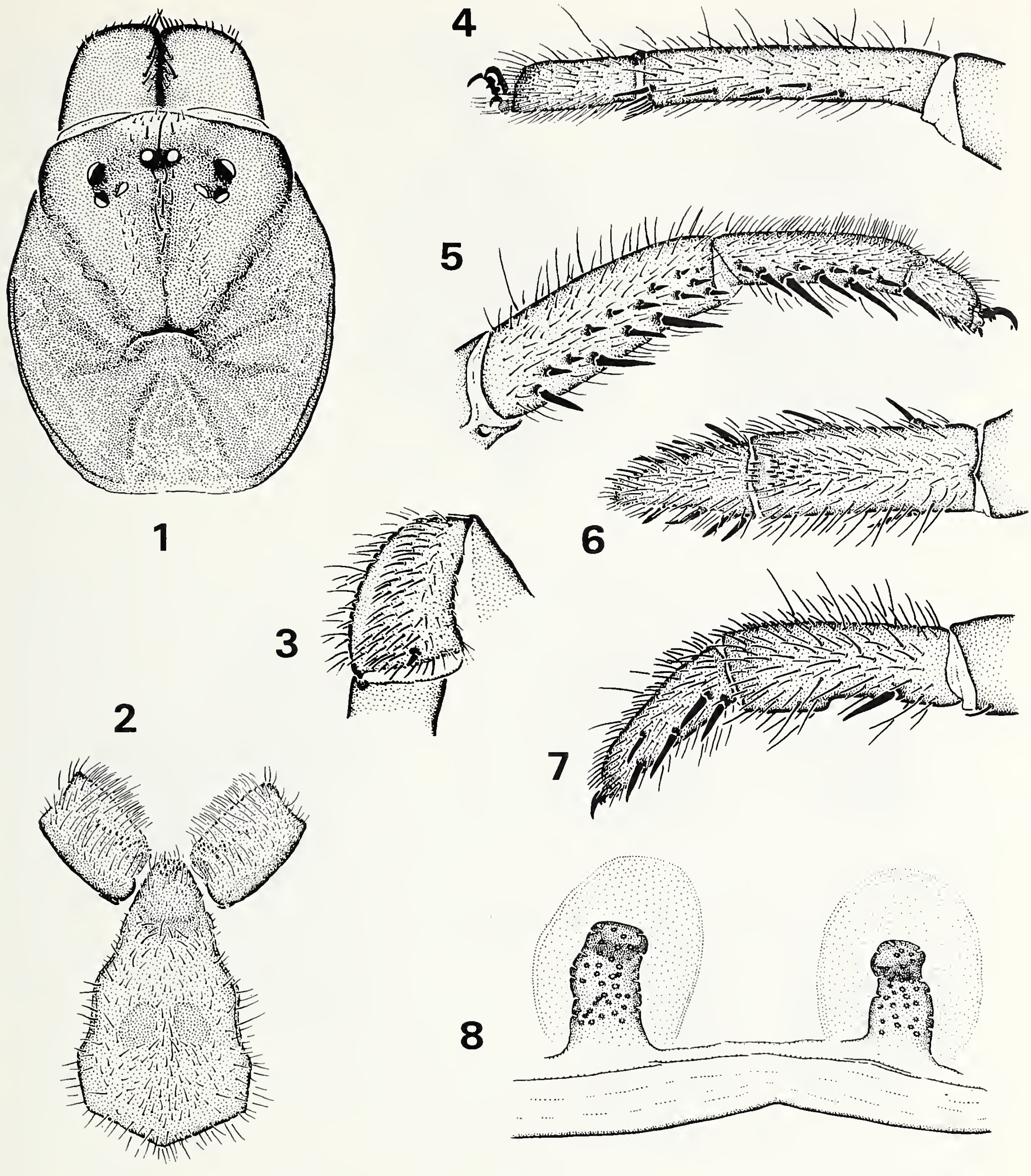
Etymology.—Pihuychén is a mythic Araucanian figure, which hides in the dark to attack people, much the way the migids are thought to capture their prey.

Diagnosis.—Females of *C. pihuychen* differ from females of both previously known species of the genus by the narrower OQ (Fig. 1), the more recurved fovea, the smaller and more numerous cuspules on the labium and palpal coxae (Fig. 2), the normal ITC on leg III, and the weaker and less numerous dorsal apical cusps on the palpal tibia (Fig. 6). The trapdoor of *C. pihuychen* (Figs. 9, 10) is more rounded, the hinge is wider, and the holding pits are smaller and more numerous than in *C. coronatus* (Fig. 11).

Female (Holotype).—Total length, 18.51. Cephalothorax (Fig. 1) 7.23 long, 6.25 wide; head convex, less elevated than in other species of the genus. Clypeus very wide; AER slightly recurved; OQ occupying 0.58 of head width. Chelicerae without rastellum, with 4 teeth on retromargin, 5 on promargin, and 15 denticles in fang furrow; anterodorsal edge of chelicerae with few strong setae forming single row. Cheliceral fangs keeled, without basal outer tooth. Labium 1.16 long, 1.36 wide, with 17 cuspules. Palpal coxae elongate, with 33 cuspules reaching middle of length. Sternum (Fig. 2) 4.53 long, 3.35 wide, separated from labium by suture, only posterior sigilla evident. Leg measurements:

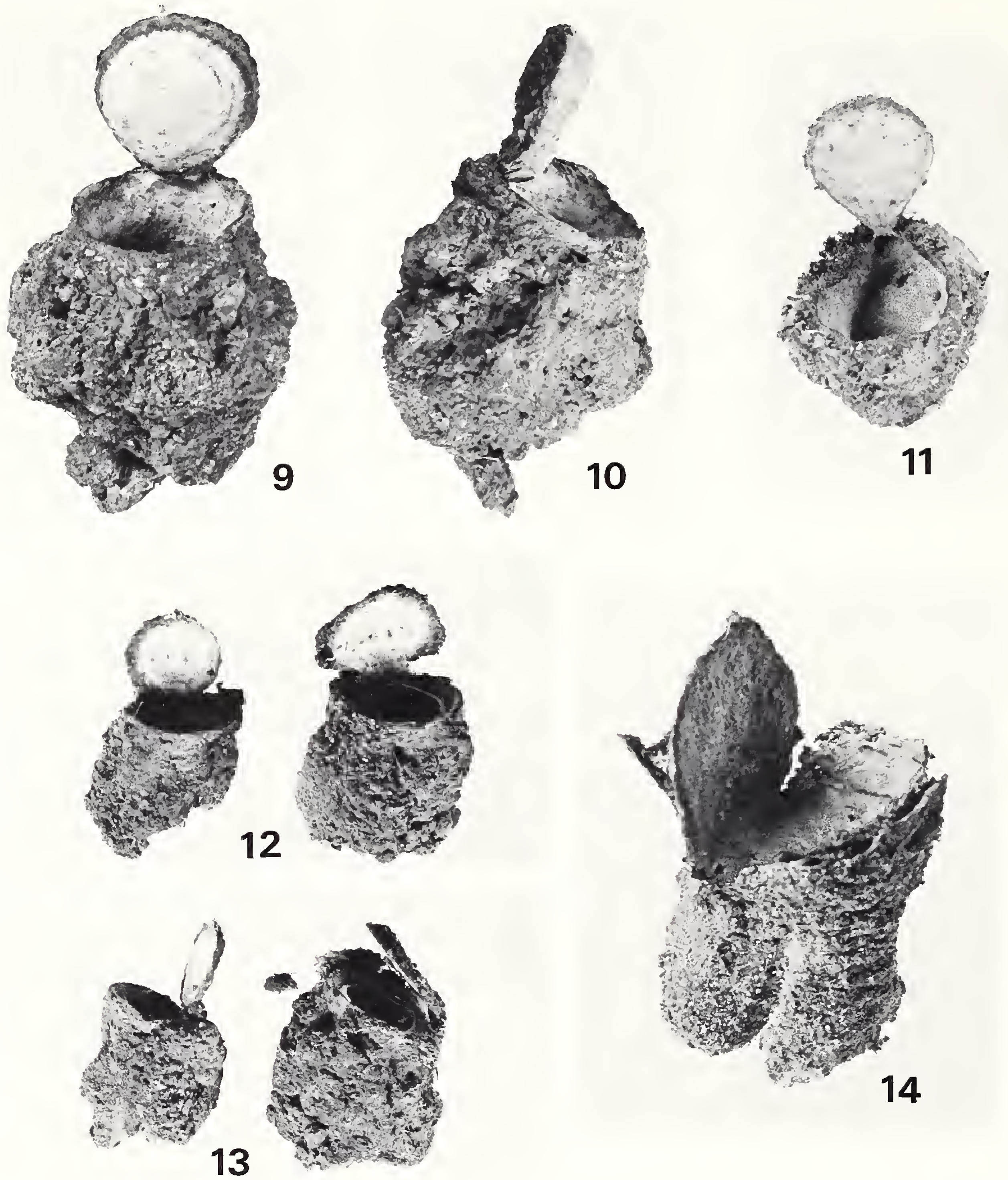
	Femur	Patella	Tibia	Metatarsus	Tarsus	Total
I	5.20	3.17	3.57	2.68	1.14	15.75
II	4.79	2.84	3.25	2.60	1.14	14.62
III	3.65	2.76	3.17	2.88	1.62	14.09
IV	5.76	3.57	4.22	4.18	1.79	19.53
Palp	3.57	1.91	2.19	—	1.79	9.46

Trichobothria: Tibiae, I, ant 4 (1:3 B), post 3 (1:4 B); II, ant 5 (1:3 B), post 4 (1:4 B); III, ant 7 (4:5 B), post 3 (1:3 B); IV, ant 3 (1:5 B), post 3 (2:5 B); palp, ant 3 (1:2 B), post 0. Metatarsi, I, 10 (1:6 A); II, 13 (1:3 A); III, 12 (2:3 A); IV, 10 (1:2 A). Tarsi, I–III, 17/18 (forming a band); IV, 9 (in a zig zag row); palp, 4 (1:3 M). Spines: all femora without spines. Patellae I and II, 1 R INF A; III, 1 P A; IV, about 50 d ant b; palp, 1-1-1 P (the second longest). Tibiae, I, 8/9 P, 15/18 R INF; II, 7 P, 11/13 R; III, about 35 p sup (1:2 a); IV, 1 v ant a; palp, 1 P (1:3 B), 1-1-1 R, about 20 d (1:4 a). Metatarsi, I, 8 P, 9/11 R INF; II, 9/11 P, 6/8 R INF; III, about 50 d ant, apical comb of 14 (in ventral half); IV, 0-1-1-1-1-1 P INF, apical ventral



Figs. 1–8. *Calathotarsus pihuychen,* female holotype. 1. cephalothorax and chelicerae, dorsal view. 2. sternum and maxillae. 3, patella III, prolateral. 4. metatarsus-tarsus IV, prolateral. 5. tibia-tarsus I, retrolateral. 6. palpal tibia and tarsus, dorsal. 7. palpal tibia and tarsus, prolateral. 8. spermathecae, dorsal.

comb of 17. Tarsi I and II, 0 P, 0 R, about 20 p inf (1:2 a); III and IV, 0; palp, 5/8 P, 4 R. Tibia III not excavated. Spines of anterior legs (Fig. 5) very elongated; third leg (Fig. 3) with many spiniform setae; fourth leg (Fig. 4) with few spines. Palpal tibia with distoventral expansion (Fig. 7) and dorsodistal group of cusps (Fig. 6). STC teeth: I, both claws TT; II, ant d-TT, post TT; III, both claws t-T-T; IV, ant t-T, post t-T-T-T; palpal claw with TT; ITC of tarsus III only slightly smaller than ITC of other legs.



Figs. 9–14. Trapdoors of Chilean Migoidea. 9, 10. *Calathotarsus pihuychen,* female holotypus. 11. *C. coronatus,* from Palmas de Ocoa, Parque Nacional La Campana, Prov. Quillota. 12, 13. *Migas vellardi,* from Playa Agua Dulce, Prov. Choapa. 14, *Plesiolena bonneti,* from Parque Nacional Fray Jorge, Prov. Limari.

PMS with 10 spigots; PLS with ca. 35 spigots (6 of them 3 times larger than the others, grouped on the apex) on apical article, ca. 25 (5 of them 3 times larger than the others, grouped on the apex) on medial article; no spigots on basal article.

Spermathecae short, thick, unbranched (Fig. 8).

Cephalothorax, legs, and chelicerae reddish brown; abdomen uniform gray.

Male.—Unknown.

Habitat.—The female holotype was collected from a burrow (containing an egg-

sac) in a steep ravine bank. This ravine leads into the Córdoba creek; many other empty burrows were found here and also along the main creek banks. The disturbed vegetation growing in the ravine and along the creek was, as usual in this area, denser than further up the banks.

Relationships.—Four characters were mentioned by Goloboff and Platnick (1987) as synapomorphies of *Calathotarsus coronatus* and *C. simoni* (the only species then known): the modified female palpal tibia bearing a distoventral expansion and a rastelliform dorsodistal group of cusps, the wide OQ, the presence of a tumescence on male chelicerae, and the bent male metatarsus I.

The modified female palpal tibia defines the group that also includes *C. pihuychen.* The narrower OQ and the less developed dorsodistal comb in the palpal tibia of *C. pihuychen* suggest that this species is the sister group of *C. coronatus* and *C. simoni.*

The intercheliceral tumescence is more widespread within the family than previously thought. It was considered absent in all migids by Raven (1985), but has been subsequently observed not only in *C. coronatus* and *C. simoni* (Goloboff and Platnick, 1987) but also in some Miginae (*Migas vellardi* Zapfe, 1961 and a specimen in the American Museum of Natural History identified by Griswold, 1987b as *M. variapalpus* Raven, 1984—probably a different species, given that the type of *M. variapalpus* lacks intercheliceral tumescence—Raven, pers. comm.). Tumescence is absent in the genus *Heteromigas* Hogg, 1902 and reportedly absent in the other Rastelloidina, except *Cyclocosmia* (Ctenizidae) and *Cataxia* (Idiopidae). If the intercheliceral tumescence is truly absent in the outgroup of the Migidae, at some level its presence defines a group within the family. The fact that *Calathotarsus* shares with other Miginae this character, absent in *Heteromigas,* suggests that *Calathotarsus* is more closely related to those other migids than to *Heteromigas.* This agrees with Goloboff and Platnick's (1987) hypothesis that the subfamily Calathotarsinae (which includes the genera *Calathotarsus, Heteromigas,* and *Mallecomigas*) is paraphyletic. At present, the level at which the intercheliceral tumescence defines a group within the family cannot be determined, but it is certainly at a higher level than the genus *Calathotarsus.* It should therefore be present in the currently unknown males of *C. pihuychen.*

Another character, the presence of a basal outer tooth in the cheliceral fang, might conflict with the intercheliceral tumescence. The basal outer tooth has been considered a synapomorphy of the subfamily Miginae (Raven, 1984, 1985; Griswold, 1987b), but an apparently homologous structure has been observed in the actinopodid genera *Actinopus, Missulena* (Raven, 1985:143) and *Plesiolena* (Goloboff and Platnick, 1987). Thus it seems equally parsimonious to regard it as a synapomorphy of Migoidea (Actinopodidae + Migidae), with loss in some migids, or as defining both the family Actinopodidae and the subfamily Miginae.

The males of *C. pihuychen* may or may not have a bent metatarsus I; no prediction is possible with regard to this character.

Distribution.—Known only from the type locality.

Material examined.—Only the type specimen.

BURROW STRUCTURE

C. pihuychen lives in burrows closed with a thick and rigid trapdoor (Figs. 9, 10). The rounded door has beveled edges and fits snugly into the burrow mouth. The

outer surface is slightly concave. The inner surface has two submarginal series of several small pits (which presumably mark where the spider inserts its fangs or claws to hold the door shut). The hinge is narrow but firmly articulated. The burrow is about 15 cm deep and 15 mm wide. It has a layer of white silk adhering to the walls.

The other Chilean species of the genus, *C. coronatus,* makes burrows quite similar to those of *C. pihuychen.* The door of this species is also thick and rigid with beveled edges. However, the hinge is much narrower (Fig. 11), and therefore the door is pointed toward the hinge. The holding pits are larger, more widely separated, and less numerous. The burrows of the Argentinian species, *C. simoni,* were succinctly described by Schiapelli and Gerschman (1975) but details of door thickness, hinge form, and holding pits were omitted. No other observations exist of burrows of this species in nature. The door constructed by a specimen (from Sierra de La Ventana, Buenos Aires, Galiano, Scioscia coll.) kept in captivity was of the thick type, rounded, with a hinge similar to that of *C. pihuychen.* The observation of this single door, constructed in a short period of time, is less reliable than observations in nature of several burrows, maintained over long periods by the spider. Nonetheless, it suggests that the very narrow hinge and distinctive shape of the doors of *C. coronatus* are autapomorphies of this species.

Two other migid genera occur in Chile; *Migas* Koch, 1837 and *Mallecomigas* Goloboff and Platnick, 1987. The burrows of *Migas* (Figs. 12, 13) are easily distinguished from those of *Calathotarsus.* The door—although rigid—is thin and without beveled edges. Being slightly larger than the burrow mouth, it lies over it instead of fitting within it. The outer surface of the door is slightly convex, and the inner surface is flat. The hinge is weaker and more loosely articulated than in the *Calathotarsus* species. The inner surface of the door has two mesal holding marks. The doors of *Mallecomigas* remain unknown.

The only other trapdoor spider recorded for Chile is the actinopodid genus *Plesiolena,* whose burrows have been described by Goloboff and Platnick (1987). The door in this genus (Fig. 14) is thin and flexible, actually consisting of a simple rounded prolongation of the thick loose paper-like silk layer that covers the walls of the burrow. The hinge is very wide and no holding marks are visible on its inner surface. The doors constructed by the other South American actinopodid genus, *Actinopus,* are thick and rigid, and have beveled edges and a narrow hinge (Goloboff, 1987; Coyle, Goloboff and Samson, in press). In the Australian genus *Missulena* the burrows are variable, with two (Main, 1956) doors, only one door, or no door at all (with the silk layer extending outside the burrow and collapsing back onto itself) (Raven, pers. comm.).

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I am deeply indebted to Claudia Szumik and Dr. Emilio Maury (Museo Argentino de Ciencias Naturales) for their cooperation in the field; to Claudio Esses for taking the burrow photographs; and to Drs. Norman I. Platnick (American Museum of Natural History), Frederick A. Coyle (Western Carolina University), Robert J. Raven (Queensland Museum, Australia), and James K. Liebherr (Cornell University) for critical reviews of the manuscript. I also wish to thank the American Museum of Natural History for Graduate Fellowship support.

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A NEW SPECIES OF *GELOTIA* (ARANEAE: SALTICIDAE) FROM SRI LANKA

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Abstract.—*Gelotia lanka* n. sp. is described from Sri Lanka based on both sexes and is distinguished from its close relative *G. syringopalpis* Wanless of Malaysia. The new taxon represents a significant extension of the range of the genus *Gelotia,* previously known only from Southeast Asia.

The Indo-Malayan jumping spider genus *Gelotia* Thorell was revised by Wanless (1984) as part of his wider review of the subfamily Spartaeinae. According to that revision the genus contains six species, three of which are known only from males while one (*G. frenata* Thorell, the type species of the genus) is known only from the female. Wanless referred to the shape of the retrolateral tibial apophysis of male palps (described as 'cap-shaped' in ventral view) as a diagnostic feature uniting the species of this genus. In *Gelotia* this apophysis is better described as a proximally dilated distinct element which is narrowly attached dorsolaterally to the tibia via a membranous region ('amorphous process' of Wanless), basally articulating with the retrolateral surface of the tibia and capable of limited independent movement. The dorsally curving embolus and anteriorly shifted distal haematodocha and embolar base seen in *Gelotia* are also shared by another spartaeine genus, *Cocalus* (Wanless, 1981), and provide evidence for a sister group relationship between these two genera, as suggested already by Wanless (1984).

The genus *Gelotia* has been thought until now to be restricted to a region extending from peninsular Malaysia through the Indonesian archipelago to New Guinea; it has not been recorded from continental Southeast Asia or from the Indian subcontinent. The discovery of a new species from Sri Lanka is therefore of great interest as it extends the range of the genus considerably. The new species is additionally noteworthy in displaying several derived features which it shares with *Gelotia syringopalpis* Wanless of West Malaysia. Among these features are the presence of a posterior ramus on the retrolateral tibial apophysis and the highly modified embolar region of the male palp and the presence of a pair of mammiform tubercles on the copulatory ducts of females. [These tubercles are not shown by Wanless in the relevant figure of *G. syringopalpis* (Wanless, 1984:179, fig. 21G) but are certainly present in that species though rather small.] The discovery of a *Gelotia* in Sri Lanka suggests that further collecting may reveal the presence of the genus also in the Indian subcontinent, in particular in the rainforest areas of the southwest and northeast. The format of the description follows Wanless (1984); actual measurements, rather than ratios, are provided, however. Museum abbreviations are as follows: AMNH (American Museum of Natural History, New York); CNMS (Sri Lanka Department of National Museums, Colombo).

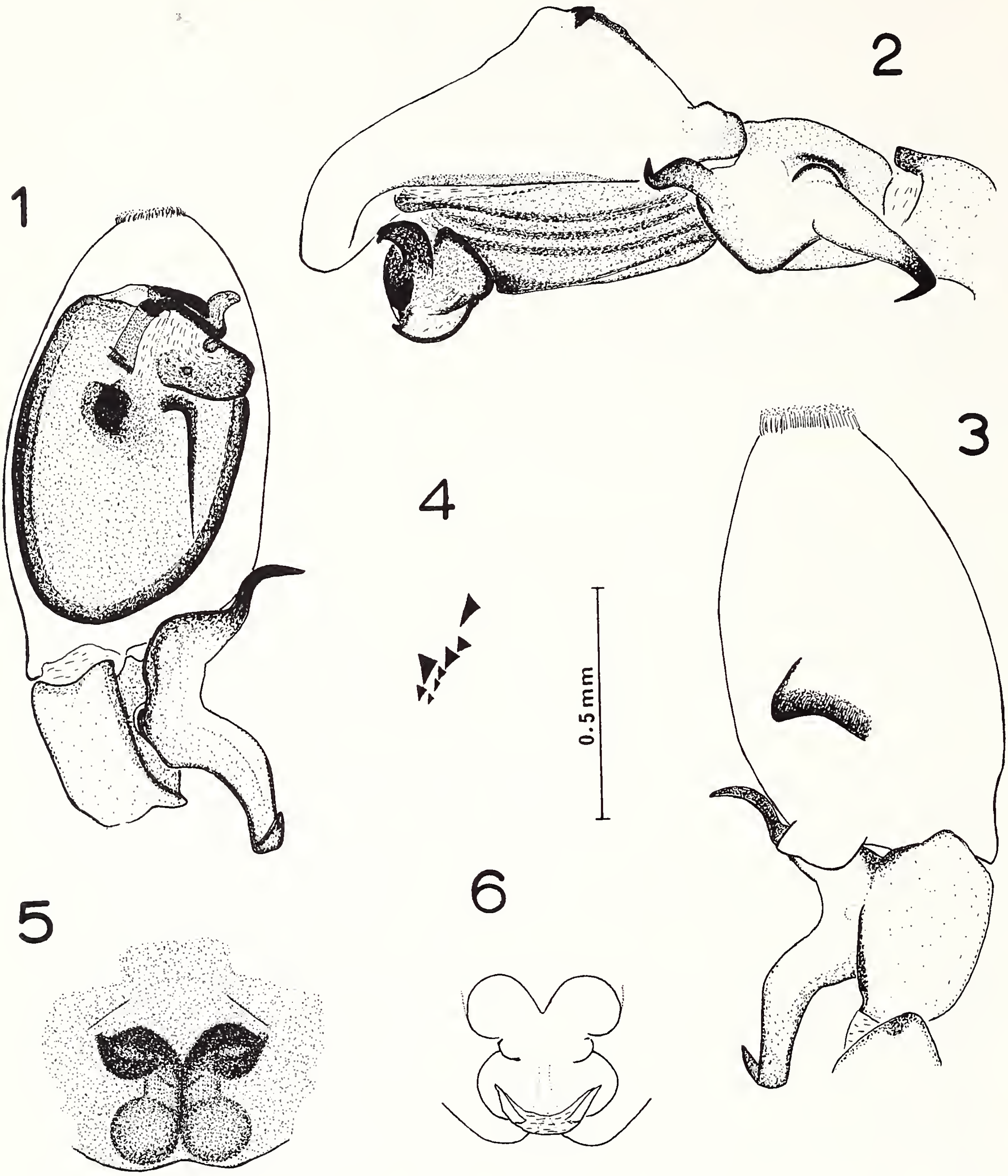
Gelotia lanka, new species
(Figs. 1–6)

Diagnosis. G. lanka appears to be closely related to *G. syringopalpis* on the basis of the biramous retrolateral tibial apophysis of males and the presence of a pair of mammiform tubercles on the copulatory ducts of females; however, it can easily be distinguished from that species by the posteriorly keeled dorsal cymbial apophysis and the different structure of the retrolateral tibial apophysis in males and the shallow, wide epigynal atrium and distally bulbous copulatory ducts in females.

Male holotype (in good condition). *Carapace:* reddish brown, with faint blackish markings; eye region lightly punctate, faintly iridescent, clothed with brownish hairs, darker on sides and thoracic region; margins narrowly blackish, pair of broad white bands above margins, narrower medial band on thoracic region. *Eyes:* encircled in black; few short setae laterally, row of setae behind anterior eyes; anteriors fringed with brown and white hairs. *Clypeus:* yellow-brown, clothed with white hairs; pair of long setae below each AME, triad between and below AME; row of white hairs at margin. *Chelicerae:* yellow-brown, tinged greyish; clothed with white hairs and setae proximally, many long fine setae distally and medially; promargin with three, retromargin with five teeth. *Maxillae and labium:* pale yellow-brown, scopulae strong. *Sternum:* yellow-brown, tinged greyish, shiny; with scattered white hairs. *Coxae:* pale yellow-brown. *Abdomen:* dorsally pale yellow-brown, greyish at sides and posterior, clothed with short setae and scattered iridescent brown hairs; ventrally whitish, tinged grey posteriorly; spinnerets pale greyish brown. *Legs:* moderately long and slender; yellow-brown, femora with dark subterminal bands; femora I retrolaterally greyish, with small tubercle (femoral organ) ventro-prolaterally; spines numerous. Spination of legs I: metatarsi v2-0-1, p1-1-0, d0-1-2, r1-1-1; tibiae v2-2-2, p1-0-1, d1-1-0, r1-0-1; patellae p0-1-0, r0-1-0; femora p0-0-1, d0-1-4. *Palp* (Figs. 1–3): retrolateral tibial apophysis biramous, basally membranous, base of anterior ramus continuous with tibia dorsally, base of posterior ramus rounded, condyle-like, articulating with socket on retrolateral face of tibia; cymbium with well-developed posteriorly keeled dorsal apophysis, proximal retrolateral flange mammiform dorsally; tegular furrow J-shaped, embolar complex hyaline.

Dimensions (mm): total length 5.25; carapace length 2.33, breadth 1.79, height 1.45; abdomen length 2.55; legs, I 6.73, II 5.64, III 5.78, IV 7.87; eyes, anterior row 1.80, middle row 1.62, posterior row 1.75; quadrangle length 1.28; diameters, AM 0.55, AL 0.31, PM 0.19, PL 0.29; interocular distances AL-PM-PL 0.40–0.37; clypeus 0.19.

Female paratype (in good condition). *Carapace:* dark reddish brown, with irregular blackish markings; eye region lightly punctate, faintly iridescent, clothed with fine translucent hairs; sides and thoracic region with dark and pale hairs; margins blackish, pair of broad white bands above margins, narrower medial white band on thoracic region. *Eyes:* encircled in black; few short setae laterally, row of setae behind anterior eyes, anteriors fringed with white and brown hairs. *Clypeus:* reddish brown; two long setae below each AME, triad between and below AME; row of white hairs along margin. *Chelicerae:* reddish brown, anteriorly convex; medially with many long setae; three promarginal and six retromarginal teeth. *Maxillae and labium:* pale reddish brown. *Sternum:* pale brown, tinged grey, shiny; sparsely clothed with white hairs.



Figs. 1–6. *Gelotia lanka,* n. sp. 1. Palp, ventral view. 2. Palp, retrolateral view. 3. Palp, dorsal view. 4. Male cheliceral dentition. 5. Epigynum, ventral view. 6. Spermathecae and ducts, dorsal view.

Coxae: similar to sternum. *Abdomen:* dorsally fawn, paler folium widened posteriorly, with two pairs of white spots; clothed with short setae and fine iridescent hairs; ventrally blackish, pair of elongate pale blotches posteriorly at sides; spinnerets grey-brown. *Legs:* dark yellow-brown, legs I-II darker, with blackish annulations; spines numerous. *Palps:* similar to legs, tibiae and tarsi with long white hairs; terminal claw present. Spination of legs I: metatarsi, v2-0-0, p0-1-0, r0-1-0; tibiae v2-2-3, p1-0-1;

patellae p1-0-1, r0-1-0; femora p0-0-1, d0-1-4. *Epigynum* (Figs. 5–6): atrium shallow, wide; spermathecae spherical, close together, copulatory ducts distally bulbous, heavily sclerotized, proximally with pair of large mammiform tubercles dorsally near spermathecae; postepigynal region with more or less triangular sclerotizations at sides.

Dimensions (mm): total length 6.2; carapace length 2.80, breadth 2.13, height 1.68; abdomen length 3.4; legs, I 7.13, II 6.38, III 6.14, IV 8.12; eyes, anterior row 2.01, middle row 1.82, posterior row 2.00; quadrangle length 1.33; diameters, AM 0.61, AL 0.35, PM 0.20, PL 0.34; interocular distances AL-PM-PL 0.43–0.41; clypeus 0.16.

Variation. Females (N = 3): total length 6.2–7.9; carapace length 2.80–3.20. Sclerotization of the postepigynal region is variable in extent, though present in all three specimens.

Distribution. Sri Lanka.

Material examined. Holotype: Opatha, Gampaha District: ♂, on vegetation, 23 November 1986 (T. Wijesiri, AMNH). Paratypes: same data as holotype: 2♀♀, 1 juv. (AMNH); Sinharaja Forest, Ratnapura District: 1♀, on vegetation, 20–23 October 1984 (D. P. Wijesinghe, CNMS).

Etymology. Named for the country in which the species was discovered; a noun in aposition.

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BOOK REVIEW

J. New York Entomol. Soc. 99(2):278–280, 1991

Invertebrates.—R. C. Brusca and G. J. Brusca. 1990. Sinauer Associates, Inc., Sunderland, Massachusetts. 875 pp. $47.50.

This book incorporates several new approaches not found in other invertebrate zoology textbooks. First, it has as one of the introductory chapters a general summary of modern systematics, including a brief examination of each of the three schools of thought: phenetics, cladistics, and evolutionary (according to the Bruscas, orthodox) taxonomy. Second, each chapter, wherever possible, includes a taxonomic history section which summarizes the major taxonomic achievements for each group. An effort was made in each case to include the latest phylogenetic tree or cladogram (the authors never make a clear distinction between the two, see below) available for each group of organisms examined. Where possible, explicit character support was indicated on the tree. The emphasis throughout the book is on the organisms themselves, and, wherever possible, their relationships to other organisms. In the last chapter, the authors present their own cladogram depicting the relationships of ". . . the major animal phyla . . ." discussed in the text. After a brief discussion, they invite . . . "[s]tudents interested in the history of life . . . to rigorously criticize our cladogram and compare it to those of other authors." (p. 899). This is a trend that should be encouraged.

The chapter on Classification, Systematics, and Phylogeny (chapter two) begins with a discussion of and definitions for the following topics: comparative biology, biological classification, nomenclature, and systematics. This is a welcome addition to an invertebrates textbook. However, it doesn't stop there. Following this is a discussion on monophyly, paraphyly, polyphyly, characters, homology, clades, grades, trees, and cladograms; more topics often not encountered in an invertebrates text. Overall, the discussion is adequate. One important point that is not mentioned, however, is the difference between discrete and continuous characters. Even at an introductory level, if one goes this deep into the subject, that difference should be stressed early and often in the discussion.

One other problem in this section is the failure to make clear the difference between a cladogram and a tree. This problem comes up again in the discussion on cladistics. At one point, they mention that ". . . cladograms may be thought of in the most fundamental way simply as synapomorphy patterns. . . ." Later in the same paragraph, ". . . the sequential branching of nested sets of evolutionary novelties . . . in a cladogram creates a 'family tree'—an evolutionary pattern . . ." (p. 33). The difference between the two is never made clear. It is important, if one is going to bring the subject up at all, to clearly define each aspect of it.

They begin their discussion of what is usually called evolutionary systematics by changing its name to orthodox systematics: "The term *evolutionary taxonomist* is a bit unfortunate because it suggests that the use of evolutionary theory is unique to this particular philosophy of classification. Hence, perhaps the phrase *orthodox taxonomy* is more appropriate" (p. 37).

Keeping in mind (and making the appropriate corrections for) the above-mentioned shortcomings, this chapter would make an adequate introduction to the study of systematics. It is a better general summary than is found in any other equivalent textbook.

However, while it is admirable to find a textbook so firmly advocating cladistics, the authors at times take a compromise approach to the subject which departs from accepted cladistic methodology. Some examples:

> In fact, many cladistic and phenetic taxonomists will argue that the process of constructing a cladogram is one of pattern analysis alone—although the pattern is presumed to be the product of the evolutionary process, reconstructing the pattern requires no prior knowledge of evolutionary mechanisms, only acceptance that evolution has occurred and is expressed in the characters that organisms possess. However, this claim ignores the fact that one cannot identify homologies or determine character state polarity without a framework of evolutionary hypotheses or assumptions [not necessary] (p. 38).

> In a majority of taxa, however, character polarity analyses have not yet been accomplished, and in these cases taxonomists have simply done the best they could, but always with the understanding that as the group became better understood their classifications would be refined or improved. Absence of reliable data on character polarity has led to the construction of many phylogenies based, at least in part, on autapomorphies and symplesiomorphies rather than solely on synapomorphies. All of these types of data have some kind of information content [albeit redundant information] and certainly should not be wholly ignored during evolutionary analyses, especially if distinct synapomorphies are few or wanting (p. 39).

Following the chapter on systematics, there are chapters on Animal Architecture and the *Bauplan* Concept (including symmetry, body cavities, feeding mechanisms, etc.) and The Metazoa: Development, Life Histories, and Phylogeny. After this, the book surveys the invertebrate phyla, beginning with the Protozoans and ending with the Chaetognaths, Hemichordates, and Chordates.

The illustrations are numerous and excellent. There are some old favorites which are seen in every invertebrate textbook, but an attempt was made to also include some older, less frequently seen drawings and some very current SEM shots. All of the illustrations are in black and white and the book is printed on off-white paper.

There are a number of minor typos in the book which is not surprising considering the massive effort which went into producing it. These will probably all be gone by the second edition. Also, the authors made an effort to include as much new material as possible on the often overlooked groups such as the pycnogonids and the tardigrades.

I'll end with a quote from their preface:

> We have tried to be as current as possible . . . but even as this book goes into production important new publications cross our desks. It has been estimated that the volume of scientific information is doubling about every ten years. A half-million nonclinical biology papers are published annually. As Professor George

Bartholomew noted, "If one equates ignorance with the ratio between what one knows and what is available to be known . . . each biological investigator becomes more ignorant with every passing day." Our goal has been to provide sufficient reference material to lead the interested student quickly into the heart of the literature for all the invertebrate phyla.

And in this they succeed admirably.—*Bonnie Bain, Department of Entomology, American Museum of Natural History, New York, New York 10024.*

ERRATUM

Correction to: Heiss, E. 1990. New apterous Carventinae from New Zealand (Heteroptera: Aradidae). J. New York Entomol. Soc. 98(4):393–401. The correct deposition for the holotypes of *Acaraptera waipouensis* Heiss (p. 397) and *Leuaptera yakasi* Heiss (p. 400) should be "New Zealand Arthropod Collection, Auckland," not "American Museum of Natural History."

INSTRUCTIONS TO AUTHORS

The *Journal of the New York Entomological Society* publishes original research resulting from the study of insects and related taxa. Research that contributes information on taxonomy, classification, phylogeny, biogeography, behavior, natural history, or related fields will be considered for publication. The costs of publishing the Journal are paid by subscriptions, membership dues, page charges, and the proceeds from an endowment established with bequests from the late C. P. Alexander and Patricia Vaurie.

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Longer manuscripts intended for submission as articles should be accompanied by a brief abstract. Footnotes should be avoided. Tables should be prepared as separate pages; they should be kept to a minimum because of the high cost of typesetting, but may be submitted as photographically reproducible material (see below). The list of references is headed "Literature Cited" and should follow the format indicated in the CBE Style Manual or as found in a recent issue of the Journal.

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CONTRIBUTIONS ON THE
NATURAL HISTORY AND SYSTEMATICS OF THE

HETEROPTERA AND COLEOPTERA

In Honor of

James A. Slater

Organized by

Jane E. O'Donnell
and
Randall T. Schuh

J. New York Entomol. Soc. 99(3):281–283, 1991

JIM SLATER, THEN AND NOW

JANE O'DONNELL AND RANDALL SCHUH

One drives just beyond Mansfield Hollow Lake in Mansfield Center, Connecticut, to find an old cape nestled among venerable sugar maples. Jim and Betty Slater have lived there for more than 30 years. Golly, part "wolf," part German shepherd, greets visitors at the door. He walked into the yard one day several years ago without a collar, and decided to make the Slaters' home his as well. Many of their other pets (6 cats, 4 tortoises, 3 snakes and a twenty year old "suwannee chicken") arrived in similar fashion.

When a visitor steps inside, there is no doubt that this is the home of collectors. Least apparent, at first anyway, is the world-class collection of Hemiptera, housed in a sunny new addition built to hold insect cabinets, file drawers, a work table, and all of the other tools a working systematic entomologist requires. It is easy to see how Jim still gets so much bug taxonomy done, working in such pleasant surroundings.

Original illustrations of hemipteran taxa adorn every wall. Jim realized early on that scientific illustrations were crucial to the quality and impact of his scientific papers. When in Europe in 1960, he became acquainted with Arthur Smith, an illustrator at the British Museum who had plenty of experience with true bugs. Arthur was already distinguished in his field, and produced many splendid pen and ink drawings of the Blissinae, now beautifully framed and proudly displayed with the work of a new generation. Jim worked closely with these talented young individuals (Molly Stock, Karen Stoutsenberger, Kathleen Schmidt, Steve Thurston, and Mary Jane Spring), and they produced the technically accurate yet aesthetically pleasing illustrations that grace his subsequent papers.

Probably even more noticeable to the first-time visitor than the bug drawings, though, is the vast array of milk glass displayed everywhere: more in one place than anyone is ever likely to encounter, except perhaps a glass museum! All the pieces are, of course, arranged systematically. The purple-slab hens are lined up next to the blue hens, which are next to the more familiar white hens. Systematic entomology shares more with "milk-glass-ology" than one might at first suspect. There are obvious parallels between these disciplines as far as acquiring new specimens goes (see Dick Baranowski's comments below), but even more fascinating is the fact that Jim has written a key to milk glass hens. Leave it to a keen taxonomic eye to be able to recognize the authentic from the copy, and to translate the relevant features into "key characters" that allow easy distinction for those with less acute "vision." Milk-glass has to be easier than the genus *Ozophora*! Like the milkglass, the cast iron trivets prominently displayed on living room and kitchen walls originally belonged to Slater's mother. Perhaps it was she who instilled the "collector's instinct" in her only child.

As a boy, Slater was already interested in the natural world, from birds to herps, especially snakes. Betty Slater remembers Jim being very interested in snakes when they met as undergraduates at the University of Illinois, and recollects that even

after her husband began work on his Ph.D. at Iowa State College, he still considered herpetology as a career. In fact, at the end of his tour of duty with the Navy during World War II, Jim brought a box of poisonous snakes back from Okinawa and gave them to a zoo in Chicago!

So Jim, under the guidance of Dr. Harry Hazelton Knight, professor of entomology at Iowa State, prepared a dissertation on the value of the female genitalia as taxonomic characters in the Miridae. He produced what is still the only comprehensive work on the subject, and played a critical role in advocating the use of genitalic morphology in bug classification. Although he has maintained an abiding interest in the Miridae, after moving to The University of Connecticut in 1953 Jim turned to the study of Lygaeidae.

When Jim started his studies of lygaeid bugs the most active worker in North America was Harry Barber, a retired New York secondary school teacher. Barber was very cooperative, and Jim's work on the Lygaeidae progressed rapidly. In 1955 Jim published his first large paper on the group, a world revision of the sedge-feeding subfamily Pachygronthinae.

Jim then set out, with support from the National Science Foundation, on his biggest single project ever, the 1,600+ page, 2 volume, *A Catalogue of the Lygaeidae of the World.* Studying literature and type specimens required an extended stay in Europe, and much travelling between major museums. He was accompanied for at least part of this time by Betty and three of their four children (Alex, Jackie, and Sam; their youngest, Lydia, not having been born yet). Imagine traipsing across Europe, from museum to museum, camping with 3 children in a Volkswagen bus! We continually marvel that something as comprehensive as the catalog could have been produced without all the modern conveniences that today we take for granted! Photocopying machines were in their infancy, personal computers had not been invented, and everything was typed or handwritten on 3 by 5 cards. The catalog was quite a feat indeed.

Jim then devoted nearly 20 years of his professional life to the study of the Blissinae. Numerous taxonomic revisions and an analysis of host-plant preferences were a prelude to his fine compendium, "Systematics, Phylogeny, and Zoogeography of the Blissinae of the World." His interest in this subfamily was piqued when he was asked to prepare the lygaeid fascicle for Lund University's series *South African Animal Life.* Based on specimens collected on the Lund University expedition in 1950–1951, this work helped focus Jim's research and field work for the coming decades.

Field work, whether in nearby colonial graveyards or far afield, has always been an important aspect of Jim's work, influencing his ideas and those of his students, and providing raw material for many taxonomic papers. Our knowledge of the Lygaeidae would be far less complete had not he and Betty undertaken what must at times have been a trying experience for both of them—an 8-month collecting trip to South Africa during 1967–1968. After all, here was the family again (this time without Alex but with young Lydia), thousands of miles from home, in a strange land accompanied by a graduate assistant whom they barely knew. Nevertheless, those eight short months yielded more lygaeids than even Jim had ever imagined. He returned to South Africa in 1970, only to have his trip interrupted in its first days by a ruptured disc in his lower back. He continued to do field work in subsequent years, visiting Australia, Panama, and the West Indies. These trips provided not only many spec-

imens of new taxa, but also valuable biological data on host plants, associations with other insects, and population numbers. Many contacts with foreign colleagues were also established, resulting in fruitful collaboration and numerous publications.

Jim has more recently devoted a good deal of time to an even more diverse subfamily of lygaeids, the primarily ground-dwelling Rhyparochrominae. He has described many new taxa, including the minute Lilliputocorini, and has produced the first tribal phylogeny of this large group.

The lygaeids are not, however, the only heteropteran group to receive his expert taxonomic attentions. Jim has long been interested in other families of bugs, as well as the Heteroptera and their evolution in general. His broad knowledge is evident in both *How to Know the True Bugs,* written with longtime friend and colleague Dick Baranowski, and the Heteroptera section of McGraw-Hill's encyclopedic *Synopsis of Living Organisms.* His 1957 paper on the Thaumastocoridae, coauthored with Carl Drake, is still the only comprehensive paper ever to appear on the family. This novel little group of bugs from South America, Australia, and India continues to fascinate Jim, and his contributions dealing with them have appeared periodically.

Jim's professional accomplishments have been widely recognized by the scientific community. He was elected president of the Society of Systematic Zoology in 1982. In 1986, the Entomological Society of America's Eastern Branch bestowed upon him him the L. O. Howard Distinguished Achievement Award for outstanding contributions in systematic entomology. Other forms of recognition are his receipt of The University of Connecticut Faculty Research Award in 1972 and his election as an honorary life member of the New York Entomological Society.

For a university professor, all of the above mentioned accomplishments would be laudable, but probably thought lacking, if they had not had an influence on others. The professional traditions of which Jim is a part will be perpetuated by his many students, some students of the Heteroptera, some not. All have benefitted from Jim's unwavering committment to the highest intellectual standards, and those who studied bugs from his amazing knowledge of the Heteroptera. Contributions by a number of former students, as well as those of other admiring colleagues, are included in the present volume.

Perhaps the best indication of colleagues' respect for Jim was the large turnout at his retirement dinner. All who attended, and all who wrote letters commemmorating the occasion, warmly congratulated Jim for his contributions to science and service to the university and broader academic community. We offer similar feelings again here, and wish Jim many more years of retirement FUN!

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JAMES A. SLATER, HERPETOLOGY'S LOSS, HEMIPTEROLOGY'S GAIN

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James Alexander Slater has been, and still is, interested in ornithology (annually participates in the Christmas bird count) and herpetology (witness the snakes, tortoises, and turtles in his den). Although he received his Bachelor of Arts degree in entomology, he strongly considered continuing his education in herpetology. So much so that he participated in reptile collecting trips in Louisiana. Fortunately for us he was offered a teaching instructorship in entomology, a lucrative (?) offer that a married graduate student couldn't turn down!

Jim actively pursues two hobbies, in addition to his interests in entomology. One is a study of burying grounds, gravestones, and gravestone carvers in Connecticut. During the course of pursuing this "hobby," often accompanied by his wife Betty, he visited more than two hundred burying grounds, many several times. This study resulted in the publication of a very fine book, The *Colonial Burying Grounds of Eastern Connecticut* (Archon Books, 1987). The first part of the book defines the major categories of eastern Connecticut burying grounds, who the carvers were, whose stones are in the burying grounds, what they carved and how their carvings may be recognized. The second part of the book describes the burying grounds, provides detailed directions for finding them and notes what particularly unusual stones may be found. In pursuing this work Jim applied his long experience in observation and analysis as an insect taxonomist to the problems of determining the origins of stones for which there is little or no written documentation. The book also has many outstanding photographs of gravestones by Daniel and Jessie Lie Farber.

His second hobby, not altogether unexpected of a systematist, is collecting milkglass. I can recall going on a "collecting trip" with Jim and Betty on a cold, rainy late fall day to a unique habitat, near Brimfield, Massachusetts, which they were sure would yield many new specimens. To me this unique habitat appeared to be a cow pasture (ample evidence) filled with row upon row of booths and vehicles loaded with whatever comes out of New England attics that collectors of all taxa might be interested in. By late afternoon the trip, I guess, could be called a success since a few boxes of various milkglass specimens were carried home. I'm sure that the Slater milkglass collection has several hundred pieces, including some quite scarce. Interestingly, Jim can, of course, inform you of the collecting details just as he can of the insect specimens he has collected in many parts of the world.

Over the past 30–35 years, I have collected with Jim in many places ranging from the northeast United States to many of the islands in the Caribbean. Many amusing and some not so amusing incidents might be recalled. I will mention a few.

A trip to several Caribbean islands, along with Dr. B. Jane Harrington who was at that time one of Jim's students, has many recollections. On Martinique we stayed in an 18th century manor house, the Manoir de Beauregard. Here we found a novel use for a fixture not common in U.S. bathrooms—the bidet. With modifications it

was a convenient place to soak grimy field clothing. We were accompanied part of the time on Martinique by Dr. Lucas Gruner. One day after a morning's collecting, Lucas directed us to a corrugated tin building on a lovely beach. Here, after a wait of perhaps an hour, we were served an excellent bouillabaisse on a crude wooden table under coconut palms. It was indeed difficult to continue collecting after such a meal. Travelling on to Guadeloupe, we were also escorted by Dr. Gruner most of the time. One of our collecting trips was up the volcano, La Soufriere. The road ends at a car park at La Savne a Mulets, at an elevation of 3,300 ft. The vegetation at this altitude is sparse as well as being wet due to the cloud cover. I don't recall collecting being particularly good, only being cold. In Point a Pitre we did take time to visit the market at the corner of rue Frebault and rue Thiers. A deep fragrance of a Creole market permeated the place. Local Creole women in madras turbans make deals over the produce they sell. The bright fabrics they wore competed with the rich colors of the papayas, bananas, pineapples, oranges and mangoes.

Dominica brings to mind a guest house, Castle Comfort, where we feasted on mountain chicken or crapaud (frog legs) and highly seasoned land crabs. While on Dominica we took time out to visit a mission school for girls which specialized in the production of woven grass items. There Jim, decided to buy a straw hat to take the place of a field hat that should have been discarded years ago. We left with Jim proudly wearing his new hat and smiling at the lilted voices of the girls singing over their weaving. When we later called at the Institute of Jamaica in Kingston to visit Tom Farr and see the collection, Jim was wearing his new hat. The day was hot and all of us were perspiring during the drive to Kingston. Upon our arrival we were greeted by Tom and taken to the insect collection room. Jim took off his hat and began to examine the material while conversing with Tom. Jim's new hat had a magenta head band that left a wide streak on his forehead! We thought it rather amusing and didn't tell Jim about it for some time! I have often wondered why Tom didn't say anything.

Later, on Jamaica, after collecting most of the day out of Linstead, we drove to Mandeville in central Jamaica in search of the Mandeville Hotel. On the way we purchased fresh fruit from a roadside stand. We found the hotel after dark. There was no one there, but the woman who evidently operated it was in a building next door. She told us to take any of the rooms (Should this have told us something?). We entered into a large room that evidently served as a lounge having scattered chairs and a few coffee tables. The bedrooms opened off of this room. After taking care of the collected material and recording the daily field notes, we retired. All night, the sounds of armies of rats scurrying about were evident; in the morning the fruit we had placed on the table was gone. Needless to say we departed in the morning. The last stay in Jamaica was at the Bamboo Lodge, in the Blue Mountains, overlooking Kingston. Joan Angus, the gruff manageress, took good care of the strange collectors. One evening she served a soursop drink as a special treat. The taste is quite unusual. Most of it was surreptitiously poured over the rail of the porch where we were dining. The next morning we found a thick white stain where it had run onto the sidewalk. It was promptly cleaned up before Joan was aware of the fate of her drink. One morning, again as a favor, Joan served something special for breakfast—kippered herring. The taste was good, but the staring eye difficult to take. I think Jim ended up covering his with a napkin and eating toast and coffee!

A few years later we took another trip to the islands accompanied by two of Jim's graduate students, Veronica Picchi and Flavia O'Rourke. I recall one day when Jim was driving on St. Lucia, we had to stop because of a large bus trying to turn around on what was a very narrow road with a steep vertical drop on one side. Jim left the car to see what progress the bus driver was making. As soon as he left the car Veronica and Flavia implored me to drive. I asked them why and they replied that everytime Jim spoke to them in the back seat of the car, he turned to face them, taking his eyes off of the road. Several months ago I visited Jim and Betty, in Connecticut, for a few days. One day we drove into Willimantic and Jim turned to say something to Betty. Her response was not the same, but Jim's habit is!

I have continued to collect actively in the Caribbean, sometimes alone and sometimes with others, but those collecting trips with Jim are among the most fondly remembered. In addition to these memories, they produced many interesting specimens, particularly in the rhyparochromine lygaeid genus *Ozophora* on which I have continued to work with Jim over the years.

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PHYLOGENETIC ANALYSIS OF CIMICOMORPHAN FAMILY RELATIONSHIPS (HETEROPTERA)

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Abstract.—A cladistic analysis of the Cimicomorpha is conducted, including 19 family-level terminal taxa and 51 characters with 127 states. The literature is reviewed and found to contain much relevant character information on gross morphology and attributes of reproduction. Previous classificatory efforts, individual characters, and new morphological information are discussed. The following sequenced classification is proposed: CIMICOMORPHA—Reduvioidea (Pachynomidae, Reduviidae); Velocipedoidea (Velocipedidae); Miriformes (Microphysoidea: Microphysidae; Joppeicoidea: Joppeicidae; Miroidea: Thaumastocoridae, Miridae, Tingidae); Cimiciformes (Naboidea: Medocostidae, Nabidae; Cimicoidea: Lasiochilidae, Plokiophilidae, Lyctocoridae, Anthocoridae, Cimicidae, Polyctenidae).

The advent of cladistics has had a profound impact on the classification of many groups, including the Heteroptera. However, many taxa have never been the subject of a detailed cladistic analysis. Schuh (1986) in a review of the subject, placed about half of the families of Cimicomorpha as *incertae sedis* because there was only one detailed analysis of all families (Kerzhner, 1981), and several of the included groups were obviously paraphyletic. Our interest in developing a comprehensive classification of the Heteroptera based on the recognition of monophyletic groups, and the opportunity to work collaboratively at the same institution, led us to this attempt at a phylogenetic classification of the Cimicomorpha.

The present paper is organized as follows: history of classification of the Cimicomorpha; brief characterization of terminal taxa used in our analysis and arguments for their monophyly; sources of character information; discussion of phylogenetic methods and results with character descriptions and a character matrix; comparison of previous and current results; classification of the Cimicomorpha; and an appendix explaining individual characters and discussion of their interpretation. Also included are figures of the labium and mesothoracic wings, cladograms of previous and current phylogenetic schemes, and character states trees for multistate characters.

The extensive work of Jacques Carayon on the morphology, anatomy, and reproduction in nearly all families of Cimicomorpha forms the foundation for much of our analysis. Without his work only a relatively superficial listing of characters would be possible. It is clear that our attempts at synthesis differ greatly from those of Carayon. This appears to result from our efforts to view characters in a transformational framework. Such an approach allows character information to be construed hierarchically, and more effectively portrayed in a phylogenetic context. Furthermore,

in our attempts to produce a phylogenetic classification, we have rejected paraphyletic groups and attempted to form all groupings on the basis of synapomorphy.

DEDICATION

This paper is written in honor of our longtime friend and colleague James A. Slater. Such recognition seems fitting, because in addition to his voluminous and seminal contributions on the Lygaeidae, his first major work on the Heteroptera concerned the Cimicomorpha, more particularly the significance of the female genitalia in the classification of the Miridae. Of still greater importance for understanding broad-scale relationships within the Cimicomorpha are his contributions on the Thaumastocoridae. On a more personal level we have always benefited from his interest in our own work, in the form of straightforward encouragement, exchange of ideas, and critical commentary. His distinguished and productive career has long served as an example, and we wish him many more productive years of enjoying his interest in the Heteroptera.

HISTORY OF CLASSIFICATION OF THE CIMICOMORPHA

The traditional classification of Dufour (1833) divided the Heteroptera into the Geocorisae, Hydrocorisae (now Nepomorpha), and Amphibicorisae (now Gerromorpha); recently it has become clear that only the last two groups are monophyletic (Rieger, 1976, and Andersen, 1982, respectively). Identification of monophyletic subgroups within the Geocorisae has been a gradual process, the major breakthroughs coming with the recognition of the Trichophora by Tullgren (1918) and later the recognition of the Pentatomomorpha (Aradidae + Trichophora) and the Cimicomorpha by Leston, Pendergrast and Southwood (1954) (for a review and presently accepted classification see Štys and Kerzhner [1975], Schuh [1986], and Insects of Australia [1991]). The Cimicomorpha as conceived by Leston, Pendergrast and Southwood (1954) is very similar to that used in this paper, except that they did not mention in which higher group the Thaumastocoridae were to be placed. The Thaumastocoridae were unequivocally associated with the Cimicomorpha by Drake and Slater (1957). The Vianaidinae (Kormilev, 1955b) were included in the Cimicomorpha, and more particularly in the Tingidae, by Drake and Davis (1960), and the Medocostidae were described and added to the group by Štys (1967a).

Some modern authors have conceived the Cimicomorpha in the same sense as Leston, Pendergrast and Southwood (1954), e.g., Miyamoto (1961), Popov (1971), Štys and Kerzhner (1975), Schuh (1979), and Kerzhner (1981), whereas other authors treated the group in a much broader sense, e.g., China and Miller (1959: fig. 1) who included the Dipsocoromorpha and Enicocephalomorpha, Wagner (1961) who included the Dipsocoromorpha, Stichel (1955) who included the Dipsocoromorpha and Leptopodomorpha, and Scudder (1959) who included the Dipsocoromorpha, Gerromorpha, Nepomorpha, and Leptopodomorpha. On the other hand, Cobben (1968, 1978) believed the Reduviidae and Thaumastocoridae must be placed outside the Cimicomorpha, and they (as well as the Pachynomidae) have been consistently omitted by Carayon (1977a, b, 1984) and Péricart (1983). Our arguments for accepting

the Cimicomorpha in the sense of Leston, Pendergrast and Southwood (but also including Thaumastocoridae) are presented below.

Although a number of family trees and narrative arguments concerning relationships within the Cimicomorpha have appeared in the literature over the decades, only two authors have published phylogenetic arguments. Schuh (1979), using data from Cobben (1978), considered the relationships of the Reduviidae, Pachynomidae, and remaining families, and Kerzhner (1981) treated all families currently placed in the Cimicomorpha. Ford (ms) analyzed data published by Carayon for the cimicoid families, and her cladogram and supporting character information were published in Schuh (1986).

TERMINAL TAXA AND ARGUMENTS FOR THEIR MONOPHYLY

In the following paragraphs we discuss the selection of outgroups used in our cladistic analysis and document the monophyly of the Cimicomorpha and terminal taxa. Examples of characters unique to each terminal taxon are provided, as well as a brief modern history of the classification of the various groups. Characters listed are usually autapomorphies and are not included in our phylogenetic analysis. Additional autapomorphies are listed in the caption to Figure 1.

Outgroups. We have used the Leptopodomorpha and a hypothetical cimicomorphan ancestor as outgroups in our analysis. Characters for the hypothetical ancestor are those found in the ground plan (see also discussion under Phylogenetic Methods). When variation for a given character occurred in the outgroup, we generally coded for the character as it occurs in the presumed ground plan for the Heteroptera. We use the term *ground plan* to mean the character set of the most recent common ancestor of a group. For example, the prepedicellite (character 6) according to Zrzavý (1991) is present in the Saldoidea and absent in the Leptopodoidea. Its absence appears to be part of the heteropteran ground plan (Zrzavý, 1991) and we have therefore coded it in this manner for the Leptopodomorpha.

Schuh (1979) regarded the Pentatomomorpha as the sister group of the Cimicomorpha. We coded a hypothetical pentatomomorphan ancestor in the matrix, but found that it was always treated as part of the Cimicomorpha, rather than an ancestor. This appears to result from the fact that not enough information is contained in our character matrix to correctly relate outgroup taxa such as the Pentatomomorpha, which share many attributes in common with phytophagous Cimicomorpha. Furthermore, there is insufficient information available in the literature to confidently determine the ground plan condition in the Pentatomomorpha for many of the characters used in our study. The question of infraordinal relationships is beyond the scope of this paper, so we have retained the outgroups specified above, because as documented below there is ample evidence showing the Cimicomorpha as monophyletic and no evidence suggesting that one of its subgroups is more closely related to the Pentatomomorpha than to the remaining Cimicomorpha. In the long run, only a study at the infraordinal level will determine whether we have rooted the cladogram correctly or not.

Cimicomorpha. A revised diagnosis of this group indicates that its members possess the following synapomorphies:

1) The ectodermal median spermatheca is nonfunctional as a sperm storage organ

and is either vestigial, modified into a vermiform gland, or entirely absent. Concommitantly, the methods of insemination and sperm storage are diverse and unique among the Heteroptera, sperm often being stored in organs evolved *de novo.* Absence of the spermatheca or its nonfunctionality as a sperm storage organ is shared only with some clearly unrelated members of the Enicocephalomorpha, Dipsocoromorpha, and a few Pentatomomorpha, viz., Aneurinae (Aradidae) (Carayon, 1954, 1955), Idiostolidae (Scudder, 1962; Schaefer, 1966), and some Oxycareninae (Lygaeidae) (Carayon, 1964). We know of no evidence suggesting that a non-functional spermatheca is part of the ground plan of any one of these higher groups. For interpretation of the modified spermatheca see discussion under character support below and of character 43 in the Appendix.

2) Eggs with micropyles which are distinct from aeropyles ("pseudomicropyles") and both arranged in a ring outside the operculum. (For the condition in other groups, see Cobben, 1968.) However, the operculum is absent in the Plokiophilidae, the micropyles are situated on the operculum of some Bryocorinae (Miridae), and are missing in several families (all cimicoid families, Pachynomidae, and Nabinae: Arachnocorini), and the Thaumastocoridae are in many respects aberrant (Southwood, 1956; Cobben, 1968).

Current knowledge of phylogenetic relationships and character distributions within the Cimicomorpha makes the status of other characters considered as synapomorphic by Leston, Pendergrast and Southwood (1954) and Sweet (ms) equivocal. Among these are: characters of the endosoma and basal apparatus of the phallus, course of the radius and media in the hind wing, common presence of the costal fracture, vesicular nature of the accessory salivary glands, common insertion of eggs into plant tissue, and egg rupture by pressure of serosa or embryonic cuticulum combined with the absence of an egg burster. Some of these characters are shared with other higher taxa, part of them being possible characters of the heteropteran ground plan. A few other potential synapomorphies for the Cimicomorpha are discussed below in connection with the results of our phylogenetic analysis.

Reduviidae. This very large world-wide group of predatory bugs has been divided into about 30 subfamilies, but following studies by Davis (1957, 1961, 1966, 1969; and others), the number has been reduced to 23 subfamilies and 33 tribes recognized by Putchkov and Putchkov (1985) and Putchkov (1987) or 25 subfamilies recognized by Maldonado (1990). The Reduviidae has been conceived as a unit by many authors, with the sometime exclusion of the Elasmodeminae and Phymatinae (Wygodzinsky 1944; China and Miller, 1959; Madonado, 1990) as separate families. Arguments for inclusion of the Elasmodeminae within the Reduviidae were made convincingly by Davis (1957) and for the Phymatinae by Carayon, Usinger and Wygodzinsky (1958), the latter argument accepted by Davis (1961), but apparently rejected by Kormilev and Froeschner (1989). Should these two subfamilies be regarded as distinct families, then at least the Holoptilinae, which also belong to the phymatine-elasmodemine clade (Carayon et al., 1958), would also have to be elevated to family rank in order to maintain a monophyletic Reduviidae. Such a splitting might also affect the rank of some other reduviid taxa, because according to Davis (1961) the Phimophorinae, Mendanocorinae, and Centrocneminae also belong to the "phymatine complex." The Emesinae have often been treated as a distinct family, but no modern specialist has done so (see e.g., Wygodzinsky, 1966). Characters distinctive

to the Reduviidae (including Elasmodeminae, Emesinae, and Phymatinae) are: prosternal stridulatory sulcus, distinctive fore and hind wing venation (Davis, 1961), consistent lack of a costal fracture, and presence of paired tubular pseudospermathecae serving the function of the spermatheca (Carayon, 1954) which is transformed into a vermiform gland. Many members of this morphologically diverse group have lost or dramatically modified certain ground plan characters, e.g., the labium is secondarily elongate and flexible in the hematophagous Triatominae and the prosternal stridulatory sulcus has been lost in some genera (Miller, 1956b).

Pachynomidae. Recognized as a family by most modern authors (e.g., Carayon and Villiers, 1968), the Pachynomidae according to Davis (1966) might even be considered as a subfamily of the Reduviidae. They were originally described in the Nabidae by Stål (1873), transferred to the Reduviidae by Carayon (1950a), and elevated to family rank by Carayon (1954). The group is pantropical with four described genera, placed in two subfamilies by Carayon and Villiers (1968): Pachynominae (*Camarochilus* Harris, 1930; *Pachynomus* Klug, 1830; and *Punctius* Stål, 1873) and Aphelonotinae (*Aphelonotus* Uhler, 1894). Its members are distinguished by their possession of trichobothria on either side of the ventral abdominal midline. In addition to a small and relatively inconspicuous prepedicellite, they have 5-segmented antennae, owing to fragmentation of the pedicel into 2 segments (as in the Pentatomoidea) combined with the occurrence of an intersegmental intrapedicelloid between the segments, which is unique among the Heteroptera (Zrzavý, 1991); the single antennal trichobothrium occurs on the distal subdivision of the pedicel (see also discussion under Prostemmatinae and character 6 in the appendix). The general facies and structure of the forewing are extremely diverse; for example, the costal fracture may be present or absent and the membrane venation may resemble that of the Nabidae or Reduviidae. The life habits are virtually unknown, and this appears (in addition to the Medocostidae) to be the only group of cimicomorphans for which larvae have never been collected.

Velocipedidae. Because of their possession of a peculiar combination of characters the members of this group have been placed in various higher groups of different ranks over time. The only genus, *Scotomedes* Stål 1873 (=*Velocipeda* Bergroth, 1891, *Godefridus* Distant, 1904), with a subgenus *Bloeteomedes* van Doesburg, 1970, was originally placed in the Nabidae (Stål, 1873), by some authors in the Saldidae (Bergroth, 1891), and later treated as a distinct family (Velocipedidae) of doubtful affinities. More recently the group has been treated as a subfamily of the Nabidae by Blöte (1945), Carayon (1970) and Kerzhner (1971, 1981). The few known species are distributed from mainland southeast Asia to New Guinea. The most obvious features unique to the group are the greatly expanded explanate exocorium in the forewing, the extremely elongate third and strikingly abbreviated fourth labial segments (also known in some Lasiochilidae), a very long costal fracture, and the presence of 3 basal, short, closed cells on the membrane with many simple veins emanating from them (Kerzhner, 1981).

Microphysidae. This group of tiny bugs is known from the Palearctic, eastern North America, and Mexico; through the courtesy of D. Jacobs (University of Pretoria) we examined several undescribed species from South Africa (Jacobs and Štys, in prep.), extending the known range into the Southern Hemisphere. At present 5 genera are recognized (*Ciorulla* Péricart, 1974, *Loricula* Curtis, 1833 [=*Microphysa* Westwood,

1834], and *Myrmedobia* Baerensprung, 1857, from the Eastern Hemisphere; and *Chinaola* Blatchley, 1928, and *Mallochiola* Bergroth, 1925, from the Western Hemisphere; see also discussion under Plokiophilidae). Family placement of the Western Hemisphere genera was a matter of dispute following their discovery because there was no general agreement on group-defining characters for many higher taxa of Cimicomorpha. The group is distinguished by: the type of alary sexual dimorphism found in the Old World species, unique venation of the forewing membrane with a single heavily sclerotized cell with a stub distilaterally, and the distal sector of R+M in the hind wing branching into a fork (shared with Nabinae only) (Davis, 1961). Also, the combination of small symmetrical parameres and a long (mirid- or anthocoridlike) costal fracture is diagnostic, although not synapomorphic for the group. Because of the minuteness and rarity of many taxa, details of morphology in the group are still in need of study.

Joppeicidae. This monotypic family contains only *Joppeicus paradoxus* Puton, 1881, a species originally placed in the Aradidae and later transferred to the Lygaeidae by Bergroth (1898), and finally incorporated in the Cimicomorpha by Leston, Pendergrast and Southwood (1954). The group is restricted to northeast Africa and the easternmost Mediterranean (Štys, 1971). Distinctive features include a pronotum with a median longitudinal carina, unique venation of the forewing membrane (Fig. 6F), simplified phallus in the form of an inverted J, and the plesiomorphic (?) presence of a well developed larval scent gland between abdominal terga 6 and 7. The major work on the morphology of the group is that of Davis and Usinger (1970). Carayon (1962a) suggested that insemination takes place in the vitellarium, as in the Cimicoidea (excluding Lasiochilidae), however, Davis and Usinger (1970) documented that it actually takes place in the distal part of the lateral oviducts and the ovariole pedicels.

Thaumastocorinae and Xylastodorinae. (*Thaumastocoridae*). We recognize the two subfamilies of the family Thaumastocoridae for purposes of this phylogenetic analysis, because although they appear to form a monophyletic group, they differ greatly in certain structures. The family includes the South Indian and Australian Thaumastocorinae (=Thaumastotheriinae) with 4 genera (*Baclozygum* Bergroth, 1909, *Onymocoris* Drake and Slater, 1957, *Thaumastocoris* Kirkaldy, 1908, and *Wechina* Drake and Slater, 1957), and the Neotropical Xylastodorinae (=Discocorinae) with 2 genera (*Discocoris* Kormilev, 1955a and *Xylastodoris* Barber, 1920). The two subgroups possess in common the often greatly expanded mandibular plates, the unique type of asymmetrical male genitalia, and the absence of external genitalia in the female. The Thaumastocorinae possess a structure we refer to as the *tibial appendix,* located distally on the foretibia, but they lack pulvilli. The Xylastodorinae are unique among the Cimicomorpha for the large pentatomomorphan-like pulvilli arising from near the base of the claws but lack the tibial appendix found in the Thaumastocorinae.

The morphology and history of classification of the family is covered by Drake and Slater (1957). Kirkaldy described Thaumastocorinae as a subfamily of Lygaeidae, and Reuter (1912) elevated it to the status of family. Barber (1920) and Kormilev (1955a) described Xylastodorinae and Discocorinae respectively; these Neotropical subfamilies were synonymized by Drake and Slater (1957). Viana and Carpintero (1981) elevated the Xylastodorinae to family status, an idea rejected by Slater and Brailovsky (1983); we agree with the latter authors. Recently Slater and Brailovsky

(1983) and Slater and Schuh (1990) have used the name Xylastodoridinae rather than Xylastodorinae; we have retained the original spelling, in spite of the fact that it might be etymologically incorrect.

Miridae. The Miridae is treated here as including the Isometopinae, following Carayon (1958) and many other subsequent authors. The Isometopinae share all of the ground plan characters of the Miridae except the plesiomorphic presence of ocelli. The family is of world-wide distribution, with 7 to 9 subfamilies and at least 30 tribes (e.g., Carvalho, 1952; Schuh, 1976); with no fewer than 10,000 described species, this is by far the largest family in the Heteroptera. Distinctive for the group are the male genitalia, always having the parameres unequally developed, the left being prominent over the right with very few exceptions, unique membrane venation with 2 cells (more rarely 1), and the several trichobothria on the meso- and metafemora. Also, the subdivided trochanters appear to be unique. Unlike most families of Heteroptera (except many dipsocoromorphans), the pretarsus shows substantial morphological variation in the Miridae (e.g., Schuh, 1976).

Vianaidinae. Owing to its distinct general facies and unique characters, this group was treated as a family by Kormilev (1955b) at the time of its original description, and later by Scudder (1959), Carayon (1962b), Štys and Kerzhner (1975), and Kerzhner (1981). We have followed Drake and Davis (1960) and Drake and Ruhoff (1965) who treated the group as a subfamily of the Tingidae. The Vianaidinae is a small Neotropical subterranean group containing 2 described genera, viz., *Thaumamannia* Drake and Davis, 1960 and *Anommatocoris* China, 1945 (=*Vianaida* Kormilev, 1955b) (originally placed in the Lygaeidae, Oxycareninae by China, 1945). Previously, the group was known only from coleopteroid specimens which exhibit the following distinctive features: reduction to complete loss of compound eyes, loss of larval scent gland 3/4, unique structure of lateral scent gland channels 4/5, and branching T-shaped metapleural ostiolar groove (Drake and Davis, 1960). They differ from the Tingidae *s. s.* by the lack of spinosity on head, lack of paranota, the elytralike corium and clavus in coleopteroid forms, lack of areolation in the hemelytra, presence of buccular bridge, long second antennal segment, and normally developed mesoscutellum. We have examined several macropterous specimens, possibly belonging to undescribed genera, from Tabago, Venezuela, and Brazil. They conform in most characters with coleopteroid specimens, but the compound eyes are normally developed. The most important characters of the macropterous forms are: ocelli absent; explanate lateral pronotal margins; posterior pronotal margin not produced posteriad; dorsum heavily punctured; legs long and thin; forewings with a strikingly raised and keel-like media; marginal venation extending to the apex of the membrane forming a sickle-shaped continuation of the corium; and a distinct and well-developed membrane with no cells, free veins, or stub.

Tingidae sensu stricto. A speciose, exclusively phytophagous group, with the recognized subfamilies Cantacaderinae with 2 tribes and the Tinginae with 2 or 3 tribes (Drake and Ruhoff, 1965). The Tingidae *s. s.* is most obviously recognized by the pronotum usually provided with paranota and one or more longitudinal carinae, the areolate forewings with a more or less uniform texture and lacking distinction between corium and membrane, head usually with spines or tubercles, mesoscutellum reduced in size or hidden by the pronotal projection, and small repellent glands distributed over the entire body surface in the larvae (Schultze, in litt.).

Medocostidae. Described by Štys (1967a) from two species of *Medocostes* from western tropical Africa, recently Kerzhner (1989) has recognized only a single species, *M. lestoni.* This group was treated as a tribe of the Velocipedinae by Kerzhner (1971) and as a subfamily of a more inclusive Nabidae by Carayon (1970) and Kerzhner (1981). Our analysis supports Štys's original assignment to family rank, the group being recognized by: absence of the costal fracture, absence of distal corial cells, absence of the buccular bridge, and uniquely by a straight labium with segment 4 longer than segments 2 and 3 combined. *Medocostes* lives on dead trees (Kerzhner, 1989). Sweet (ms) suggested a possible hematophagous habit while Kerzhner (1989) suggested predation on subcorticolous insects. However, the structure of the labium suggests that *Medocostes* may not be predaceous.

Nabidae sensu stricto. We use this family group name to include only the Nabinae and Prostemmatinae of Carayon (1970) and Kerzhner (1981), authors that have used it in a much broader sense to include also the Medocostidae and Velocipedidae. The Nabinae and Prostemmatinae are held together by the structure of the labium, venation of the membrane, and particularly by the presence of fossettes parastigmatiques and Ekblom's organ. Nonetheless, we have treated them as separate entities in our analysis, as part of our effort to recognize a monophyletic Nabidae and because each group possesses unique characters.

Nabinae. Kerzhner (1981), in his World classification, recognized four tribes, viz., Arachnocorini, Carthasini, Gorpini, and Nabini (=Arbelini and Metatropiphorini); these tribes had often been regarded as distinct subfamilies in the Nabidae (e.g., China and Miller, 1959). The group is speciose, of world-wide distribution, and of quite diverse habits. It has usually been recognized on the basis of negative features, such as the lack of scutellar trichobothria (in contrast to the Prostemmatinae), none of the labial segments extremely long or short (in contrast to the Medocostidae and Velocipedidae), and a consistent lack of the costal fracture. Positive features include: the presence in the ground plan of fossettes parastigmatiques on many abdominal segments; the presence of Ekblom's organ associated with 30–40 stiff setae on the apex of the hind tibia of the male (this large setal number being unique to the group); a branching distal sector of R+M in the hind wing (a similar condition occurs also in the Microphysidae and Pentatomomorpha); and the dorsal position of the posterior foramen of the pygophore (Kerzhner, 1981). Many members of the Nabinae diverge from the ground plan of the subfamily; nonetheless, the group has a general habitus of elongate, often nearly parallel-sided, weakly sclerotized insects with a slender, anteriorly projecting head and a relatively long, thin, curving labium.

Prostemmatinae. Many members of this group have a facies similar to the Pachynomidae, although many important features distinguish them. Both groups have apparently 5-segmented antennae. Zrzavý (1991) has shown that only in Pachynomidae are the antennae truly 5-segmented, by virtue of a subdivided pedicel, whereas in Prostemmatinae the prepedicellite is long and conspicuous (see discussion under Pachynomidae and character 6 in Appendix). Early authors often placed the Pachynomidae within the Prostemmatinae, but most recent authors have separated the 2 groups and included the Prostemmatinae within the variously conceived Nabidae. Kerzhner (1981) in his World classification recognized five genera of prostemmatines, placed in two tribes, Prostemmatini (*Alloeorhynchus* Fieber, 1860; *Pagasa* Stål, 1862; *Prostemma* Laporte, 1832) and Phorticini (*Phorticus* Stål, 1860; *Rhamphocoris* Kir-

kaldy, 1901). The family is of world-wide distribution with the greatest diversity in tropical regions. Unique features of the Prostemmatinae are: 1–7 pairs of trichobothria located on the lateral margins of the scutellum (Carayon, 1970) and the caudal or ventral position of the posterior foramen of the pygophore (Kerzhner, 1981). The Prostemmatinae further differ from the Nabinae *s. s.* by having fewer than 10 setae (associated with the presence of Ekblom's organ) on the apex of male hind tibiae (in contrast to the large numbers found in the Nabinae), and by having the fossettes parastigmatiques (if present) uniquely limited to abdominal segment 3. In contrast to the Nabinae which live mostly on vegetation, indiscriminately feeding on soft-bodied insects, the Prostemmatinae are specialized ground-dwelling predators of other heteropterans (Kerzhner, 1981).

Cimicoid families. Most modern authors have recognized 3 families, viz., Anthocoridae, Cimicidae, and Polyctenidae, within this subgroup of cimicomorphans; recently the Plokiophilidae have been added (Carayon, 1974). Nevertheless, Southwood and Leston (1958) noted that the Anthocoridae is not a monophyletic group and in their treatment of the British fauna subsumed its members under a broadly conceived Cimicidae. Carayon, over a period of 3 decades, elucidated the peculiarities of anatomy, reproduction, and life history of the cimicoid complex, offering major summaries of his work in a classification of the Anthocoridae (Carayon, 1972a) and a review of traumatic insemination (Carayon, 1977a). Ford (ms), using the extensive data of Carayon, concluded as did Southwood and Leston, that the Anthocoridae in the traditional sense, and as considered by Carayon (1972a) and Péricart (1972), were paraphyletic. Ford's excellent English language summary of the situation, suggesting that not only Cimicidae, but also Polyctenidae and Plokiophilidae, are subgroups of the classical Anthocoridae. The cladogram and character distributions from Ford's unpublished work were presented by Schuh (1986), who concluded that if we are to accept the easily diagnosed Plokiophilidae, Polyctenidae, and Cimicidae, we must break the classical Anthocoridae into at least 3 families, viz., Lasiochilidae, Lyctocoridae, and Anthocoridae *s. s.* This is the scheme we have followed in our analysis. The recognition of monophyletic groupings within the cimicoid lineage is the only difference with regard to terminal taxa our study and that of Kerzhner (1981).

Lasiochilidae. Lasiochilid genera have been placed in the Anthocoridae by all modern authors. Carayon (1972a) established a separate subfamily to accommodate them. The group is widely distributed but seems to be most diverse in tropical areas, particularly in the New World, and is almost absent from the Palearctic. The general facies of the Lasiochilidae are similar to the Lyctocoridae and Anthocoridae *s. s.*, the males having asymmetrical genitalia with the right paramere greatly reduced, but in contrast to the those groups there is no hemocoelic insemination, and as opposed to other cimicoid groups the spermatheca is in the form of a vermiform gland, as also found in many other non-cimicoid cimicomorphans. The presence of only a single pair of dorsal laterotergites associated with abdominal segments 1 and 2 (all other abdominal segments having a simple tergal plate) is apomorphic for the group (for other characteristics see Carayon, 1972a).

Plokiophilidae. This group of tiny predators was first recognized as distinct family by Carayon (1962a; see also Štys, 1962, 1967b); they were previously treated as members of the Microphysidae (China and Myers, 1928; China, 1953). Currently

two subfamilies—Plokiophilinae (Afrotropical, Madagascan [Štys, unpubl.], and Neotropical: *Lipokophila* Štys, 1967; *Plokiophila* China, 1953; *Plokiophiloides* Carayon, 1974) and Embiophilinae (Pantropical: *Embiophila* China, 1953)—are recognized (Carayon, 1974; Ford, ms). Ford (ms) suggested that a distinct subfamily should be established for *Lipokophila.* The monophyly of the group is based on: the structure of the male genitalia with the often elongate tubular pygophore, long symmetrical to weakly asymmetrical slender spiniform parameres, slender partially-coiled phallus, the females with a greatly reduced ovipositor, and the distinctive corial glands on the forewings (Carayon, 1974). In at least some Plokiophilidae the phallus is used in a unique way for symmetrical penetration of the female abdominal dorsum during repeated attempts at copulation (Carayon, 1977a). The life habits of this family are unique among the Cimicoidea, with members of the Embiophilinae living in the webs of Embiidina and those of Plokiophilinae exclusively inhabiting the webs of spiders (China and Myers, 1928; Carayon, 1974; Edgerly, 1987; Eberhard et al., in prep.).

Lyctocoridae. The Lyctocorinae of Carayon (1972a) is an omnibus paraphyletic assemblage. We restrict this group name to the tribe Lyctocorini of Carayon, including only the genus *Lyctocoris* Hahn, 1835 (Ford [ms] included here also the genus *Astemmocoris* Carayon and Usinger, 1965, regarded as Lyctocorinae *incertae sedis* by Carayon [1974]), and place all other members of Carayon's Lyctocorinae in a more restricted Anthocoridae. The group is most speciose in the Northern Hemisphere with a few species known from other regions. The left paramere in the male does not serve as a copulatory organ for penetration of the female body wall, as opposed to the situation in the Polyctenidae, Cimicidae, and most Anthocoridae. Apomorphies include: presence of genital apophysis on sternum 7 of the female, and seminal conceptacles formed by the epithelium of the genital duct in contrast to the Polyctenidae, Cimicidae, and Anthocoridae where they are formed by the so called *hemochrisme* in the peritoneal sheath of the ovariole.

Anthocoridae. We use the name Anthocoridae in a restricted sense, recognizing a monophyletic, or at least not grossly paraphyletic, group. Ford's (ms) cladogram offered two classificatory alternatives: one, that the Xylocorini and Almeidini are part of the Cimicidae, or that the Cimicidae and Anthocoridae (less Lasiochilidae and Lyctocoridae) should be combined into a single family, a solution more similar to that proposed by Southwood and Leston (1958). The former solution offers greater stability of nomenclature, but a final resolution of this problem will require further study of structural variation in these groups to determine which taxa placed in the Anthocoridae by us should be included in the Cimicidae. We include in the Anthocoridae the following suprageneric taxa recognized by Carayon (1972a): Xylocorini, Almeidini, Dufouriellini (=Cardiastethini), and Scolopini (including Scolopina, and Caliobina) of the Lyctocorinae *sensu* Carayon, and all tribes of the Anthocorinae *sensu* Carayon (Blaptostethini, Anthocorini, Oriini). This is a large and diverse group of world-wide distribution, defined by the presence of seminal conceptacles formed from *hemochrisme* and the absence of characters unique to the Cimicidae. As with the Polyctenidae and Cimicidae, members of the Anthocoridae (except Anthocorini and probably Scolopini) have the left paramere modified into a copulatory organ which penetrates the female body wall (Carayon, 1972a; Péricart, 1972).

Cimicidae. Conceived by most modern authors in a restricted sense and as rec-

ognized here, this group includes only ectoparasites of bats, man, and some birds (e.g., Usinger, 1966). It appears to be most closely related to one of the subgroups of Anthocoridae *s. s.* Ford's (ms) analysis of Carayon's data indicated that the Cimicidae are the sister group of the Xylocorini and possibly Almeidini, here placed in the Anthocoridae (see also comments under Anthocoridae). The Cimicidae were monographed by Usinger (1966), who recognized 6 subfamilies. The group is worldwide in distribution, with the greatest diversity in the tropics. The monophyly of the Cimicidae is documented by: the loss of ocelli, micropterous condition of forewings, temporary parasitism of homeothermous vertebrates associated with hematophagy, dilated anteclypeus, and broadly flattened body. This is the group in which traumatic insemination was first noted and for which the mechanisms of the unusual method of fertilization were first studied in detail (see Carayon in Usinger, 1966).

Polyctenidae. This unusual group of permanent bat ectoparasites has structural modifications presumably associated with its life habits. Giglioli (1864) described *Polyctenes molossus,* the first known species of the family, placing it in the Nycteribiidae (Diptera); ten years later Westwood (1874) placed it in the Anoplura. It was some time before the heteropteran affinities of the group were recognized. Maa (1964) subdivided the family into the Polycteninae (tropical areas of the Old World: *Polyctenes* Giglioli, 1864; *Eoctenes* Kirkaldy, 1906) and Hesperocteninae (pantropical: *Androctenes* Jordan, 1912; *Hesperoctenes* Kirkaldy, 1906; *Hypoctenes* Jordan, 1922). The ventral laterotergites are separate from the mediosternal plate, and the method of traumatic insemination is essentially like that of Cimicidae and Anthocoridae, with the left paramere in the form of a copulatory organ, but penetration is via the metacoxal membrane as opposed to the abdominal wall. Some of the numerous apomorphies include (Ferris and Usinger, 1939): presence of ctenidia, complete absence of compound eyes, labial insertion shifted caudad onto the ventral surface of the head, neotenous aptery, only 3 larval instars (Štys and Davidova-Villímová, 1989), 4-segmented middle and hind tarsi in adults (3-segmented in larvae), and annulated tibiae. Dorsal abdominal scent glands are absent in the larvae of many species (Ferris and Usinger, 1939; pers. obs.), but they were observed by Ferris and Usinger (1945) in larvae of *Hesperoctenes eumops* and 2 unidentified larvae from Brazil. We have observed that at least some polyctenids (e.g., *Eoctenes spasmae*) have a first abdominal sternum developed as a vaguely delimited semisclerotized pilose plate contrasting with the sharply delimited second abdominal sternum. This may represent the neotenous retention of larval morphology and is unique among the Cimicomorpha.

SOURCES OF CHARACTER INFORMATION

We have relied heavily on the published literature as a source of data. References of particular importance were: I. M. Kerzhner's (1981) monograph of the Palearctic Nabidae; numerous papers by J. Carayon dealing with morphology, reproduction, and classification in the Cimicoidea, Prostemmatinae, and Pachynomidae; and papers authored or coauthored by N. T. Davis dealing with comparative morphology of several cimicomorphan families.

Kerzhner's (1981) work represents the most comprehensive attempt to develop a phylogeny for the Cimicomorpha because he dealt with all currently included families, he presented his data in such a fashion that all attributes could be assigned to all

taxa, and his results were in the form of a more or less easily interpretable cladogram. Although we have adopted many of the characters (see characters 0, 3, 5, 16, 17, 19, 21, 22, 29, 30, 36, 37, 39, 41, 43, 49, 50) employed by Kerzhner (1981), we have not used all of them in exactly the same form as published by him, because some, such as labium suited for different types of feeding behavior, could not be satisfactorily interpreted by us, and others (e.g., membrane venation) seemed to be coded in such a way as to introduce some prior conclusion about relationships within the Cimicomorpha. We did not use the position of the hypocostal lamina because its states could not be precisely defined, and the character describing early or late maturation of trophocytes was known from too few taxa. Schuh (1986: caption to fig. 6) misstated Kerzhner's character 3 as "gula absent"; it should have read "buccular bridge absent."

We have used Ford (ms) as an aid in synthesizing the contributions of Carayon on the Cimicoidea *s. s.* Schuh (1986: caption to fig. 8) transcribed in error Ford's character 46, which should have read "double copulatory tubes in female," not in male. Certain aspects of abdominal morphology were suggested as characters in a yet unpublished manuscript by M. H. Sweet.

There are a number of characters or character systems mentioned in the literature which we have not included in our analysis. First, information on the male genitalia in the noncimicoid Cimicomorpha has never been presented in a format suitable for phylogenetic analysis; a modern comparative study is badly needed because the only comprehensive work available is the paper by Singh-Pruthi (1925) which does not meet modern standards. Second, certain information provided by Cobben (1978: tables 5, 6) and later reanalyzed by Schuh (1979), was not documented on a family by family basis for many of the nonreduviid families, and could not be confirmed by us without extensive anatomical studies. And third, although included in the matrix, rotatory and cardinate coxae, as originally recognized by Schiødte (1870), proved impossible to define in an objective way. When included in our computations this character produced variable results, and we have therefore treated it as inactive (see character 18 below).

Information concerning ovariole, testis follicle, and chromosome numbers, as well as other aspects of general internal anatomy have been used by various authors to suggest relationships among certain families of Cimicomorpha and as well as other Heteroptera. We have not included most of these data because in many cases information about them is too scanty and in others intragroup variation is so great that application at the family level is inappropriate.

PHYLOGENETIC METHODS

We would observe that in an ideal situation a higher taxon would be recognized as natural by a character unique to it and the character would be present in an identical form in all constituent subgroups; the more such apomorphies found for a group, the stronger the support for its monophyly. This is indeed the situation for some groups and some characters within the Cimicomorpha. However, the situation is often less clear cut, with many character states showing homoplasy within the group, and seemingly existing in other infraorders of the Heteroptera. Thus, rather than attempting a classical Hennigian analysis in which the monophyly of recognized groups might be based on a few uncontradicted characters, we have assembled as much character information as possible and employed a computer-based phylogenetic

approach in the application of parsimony as an arbiter amongst possible phylogenetic patterns. We do this for two reasons: first, the number of possible phylogenies is reduced to some finite number that have been objectively selected; and second, the most parsimonious solution represents the most economical explanation of the character data for the cladogram and its corresponding hierarchic classification (Farris, 1979, 1983).

Cladograms presented in this study were produced using HENNIG86, an IBM PC based phylogenetics package written by J. S. Farris. It contains a number of parsimony algorithms for the production of cladograms, as well as other utilities for data and cladogram manipulation. Most of our analyses used a combination of the *mh** and *bb** algorithms (heuristic with branch swapping; see Fitzhugh, 1989), intended—but not guaranteed—to find all most-parsimonious solutions, and the results presented were verified as exact solutions using the *ie* algorithm (iterative enumeration, providing all possible most parsimonious solutions).

Cladograms and characters can be readily characterized by 3 attributes: *length*—the number of steps (character-state changes) required to fit the data to the tree; *consistency index* (ci)—the ratio of the minimum number of steps for a character (or all characters) to the actual number of steps on the tree, with a value of 1.00 indicating perfect fit; and *retention index* (ri) (see Fitzhugh, 1989; Farris, 1989)—a measure of synapomorphy, with a value of 1.00 indicating a character all of whose states are consistently distributed on internal nodes of the cladogram and a value of 0.00, indicating a character which has no synapomorphy content (although characters present in a single terminal taxon have a value of 1.00). As mentioned above, we used 2 outgroups, which allowed for the precise determination of the position of the root of the cladograms produced by HENNIG86.

We used the successive approximations weighting approach of Farris (1969; see also Carpenter, 1989) to select among equally parsimonious cladograms derived from the same data on the basis of which were supported by characters of highest consistency. The details of this method as implemented in HENNIG86 are described by Fitzhugh (1989).

Much of the character information included in our study could be coded in a two state format, such that both the primitive and derived conditions represented a distinct structural or functional type, with the condition found in the outgroup being coded as zero (Tables 1, 2). Other character information benefitted from being coded in a multistate format (Fig. 2). In some cases multistate characters could be coded in a linear format with the outgroup condition as zero or as one of the states lying between the end points of the series such that the character branches on the cladogram. Other multistate characters required coding in a more complex branching format. Because HENNIG86 does not directly support complex branching characters we coded characters 19, 21, 22, 34, 37, 43, and 47 in an additive binary format (Farris et al., 1970) shown in Table 2. We present character-state trees for all multistate characters in Figure 2 to assist the reader in understanding the topology of the characters on the cladogram. Mickevich (1982) and Mickevich and Weller (1990) have argued for the inclusion of reciprocal illumination in the analysis and coding of multistate characters. We have adopted much of their approach in an attempt to produce transformation series that allowed for greatest congruence and provide maximum information for all characters being analyzed. Thus, some readers may find

our treatment of certain character information at variance with traditional interpretations found in the heteropterological literature. At various places in the present paper we comment on the consequences of our interpretations.

Those character states which could not be coded (e.g., venational attributes in the Polyctenidae) are indicated by a dash in Tables 1 and 2; those about which we lacked information by a question mark.

Character 18 (coxal types) was treated as inactive, and not included in the final result.

PHYLOGENETIC ANALYSIS

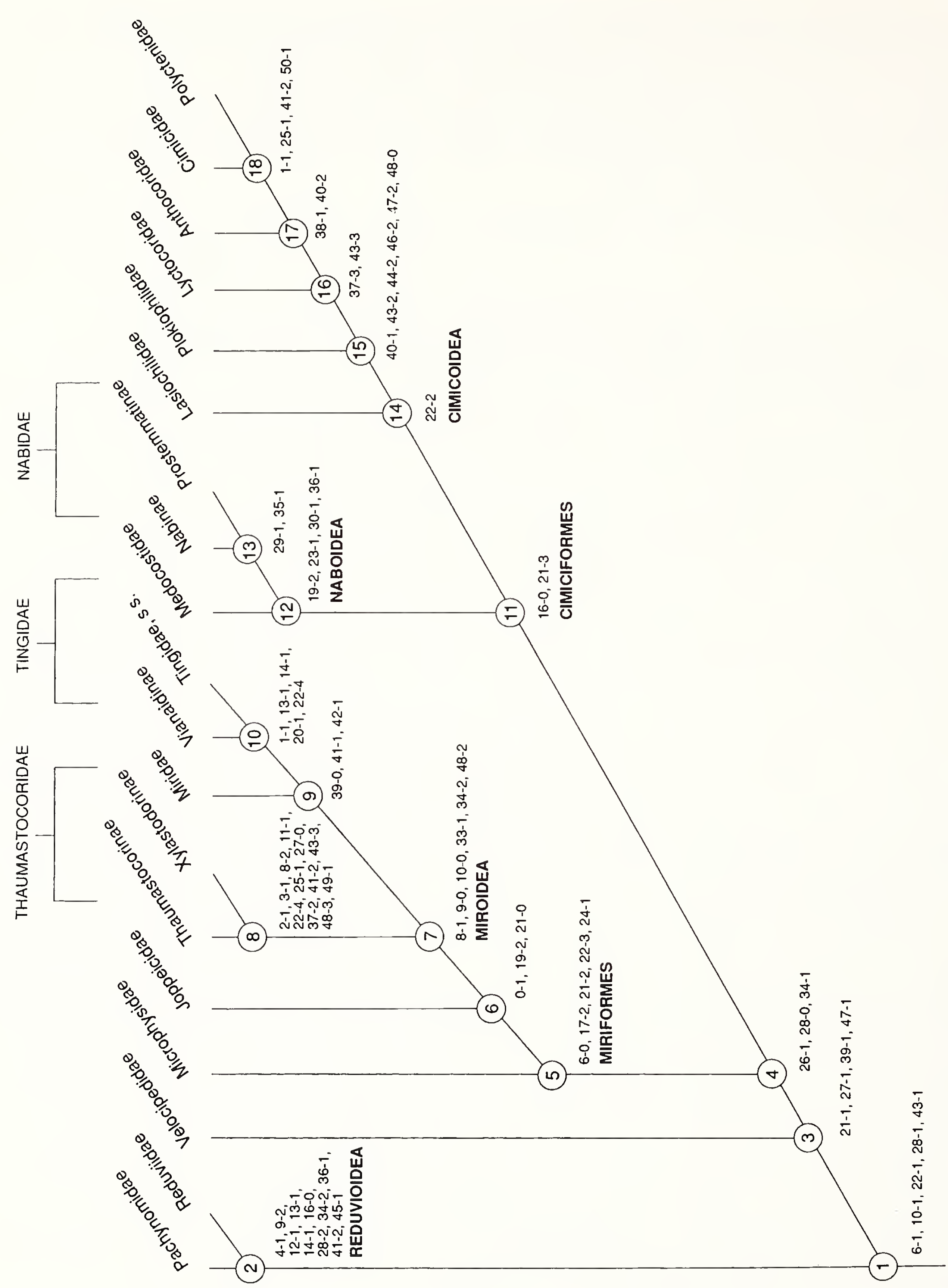
Results of analysis of newly developed data. Character information for this study is presented in the form of a matrix in Tables 1 (linear coding) and 2 (additive binary coding of some multistate characters), with 19 terminal taxa, 2 outgroups, and 51 characters and 127 states; character descriptions and pertinent statistics are given in Table 3; character state trees for multistate characters are given in Figure 2. Explanatory notes and literature references for individual characters are given in the Appendix. In many cases we have resolved ambiguous statements in the literature or clarified variation in family-level groups by examination of specimens. Some characters included in Tables 1, 2 and 3 do not define inclusive groups; nonetheless, we have retained these autapomorphies in the matrix to give our colleagues a more thorough appreciation of the information which we analyzed as well as to give a more precise demonstration of which attributes actually define groups and which do not.

Figure 1 gives the results of our analysis of the data coded in additive binary format as shown in Table 2. This cladogram is one of 2 found and the one to be preferred as determined by successive weighting (length = 156; consistency index = 49; retention index = 68). Specification of the hypothetical ancestor or the Leptopodomorpha as the outgroup made no difference in the results produced by HENNIG86.

Reanalysis of Kerzhner's data. Because part of the impetus for the present paper derived from work of Kerzhner (1981), we sought to determine whether his cladogram (redrawn by us as Fig. 3; see also Schuh, 1986: fig. 6) represented the most parsimonious solution for his data. This was accomplished by constructing a matrix using the distributions as indicated on his published diagram and confirming them by reference to his character descriptions and text discussion. We fitted Kerzhner's data to his own tree, a process which produced a cladogram of a length of 66 steps, with a consistency index of 42 and a retention index of 63. Our computations using the *ie* algorithm of HENNIG86 on the matrix of Kerzhner's data produced 24 trees from which one (Fig. 4) was selected through the use of successive weighting as showing the strongest support from the data (length = 64; consistency index = 43; retention index = 65). Note the difference in topology of the 2 trees (discussed below), and that Kerzhner's tree is slightly longer and has a lower consistency index.

COMPARISON OF CURRENT RESULTS WITH THOSE OF PREVIOUS AUTHORS

Comparison of our results with those of other authors can be made in two ways: topology of cladograms (monophyletic groups in common) and character support for groupings—whether the same or different—in the schemes being compared.


Pachynomidae
Reduviidae
Velocipedidae
Microphysidae
Joppeicidae
Thaumastocorinae
Xylastodorinae
Miridae
Vianaidinae
Tingidae, s.s.
Medocostidae
Nabinae
Prostemmatinae
Lasiochilidae
Plokiophilidae
Lyctocoridae
Anthocoridae
Cimicidae
Polyctenidae
THAUMASTOCORIDAE
TINGIDAE
NABIDAE
1
6-1, 10-1, 22-1, 28-1, 43-1
2
4-1, 9-2, 12-1, 13-1, 14-1, 16-0, 28-2, 34-2, 36-1, 41-2, 45-1
REDUVIOIDEA
3
21-1, 27-1, 39-1, 47-1
4
26-1, 28-0, 34-1
5
6-0, 17-2, 21-2, 22-3, 24-1
MIRIFORMES
6
0-1, 19-2, 21-0
7
8-1, 9-0, 10-0, 33-1, 34-2, 48-2
MIROIDEA
8
2-1, 3-1, 8-2, 11-1, 22-4, 25-1, 27-0, 37-2, 41-2, 43-3, 48-3, 49-1
9
39-0, 41-1, 42-1
10
1-1, 13-1, 14-1, 20-1, 22-4
11
16-0, 21-3
CIMICIFORMES
12
19-2, 23-1, 30-1, 36-1
NABOIDEA
13
29-1, 35-1
14
22-2
CIMICOIDEA
15
40-1, 43-2, 44-2, 46-2, 47-2, 48-0
16
37-3, 43-3
17
38-1, 40-2
18
1-1, 25-1, 41-2, 50-1

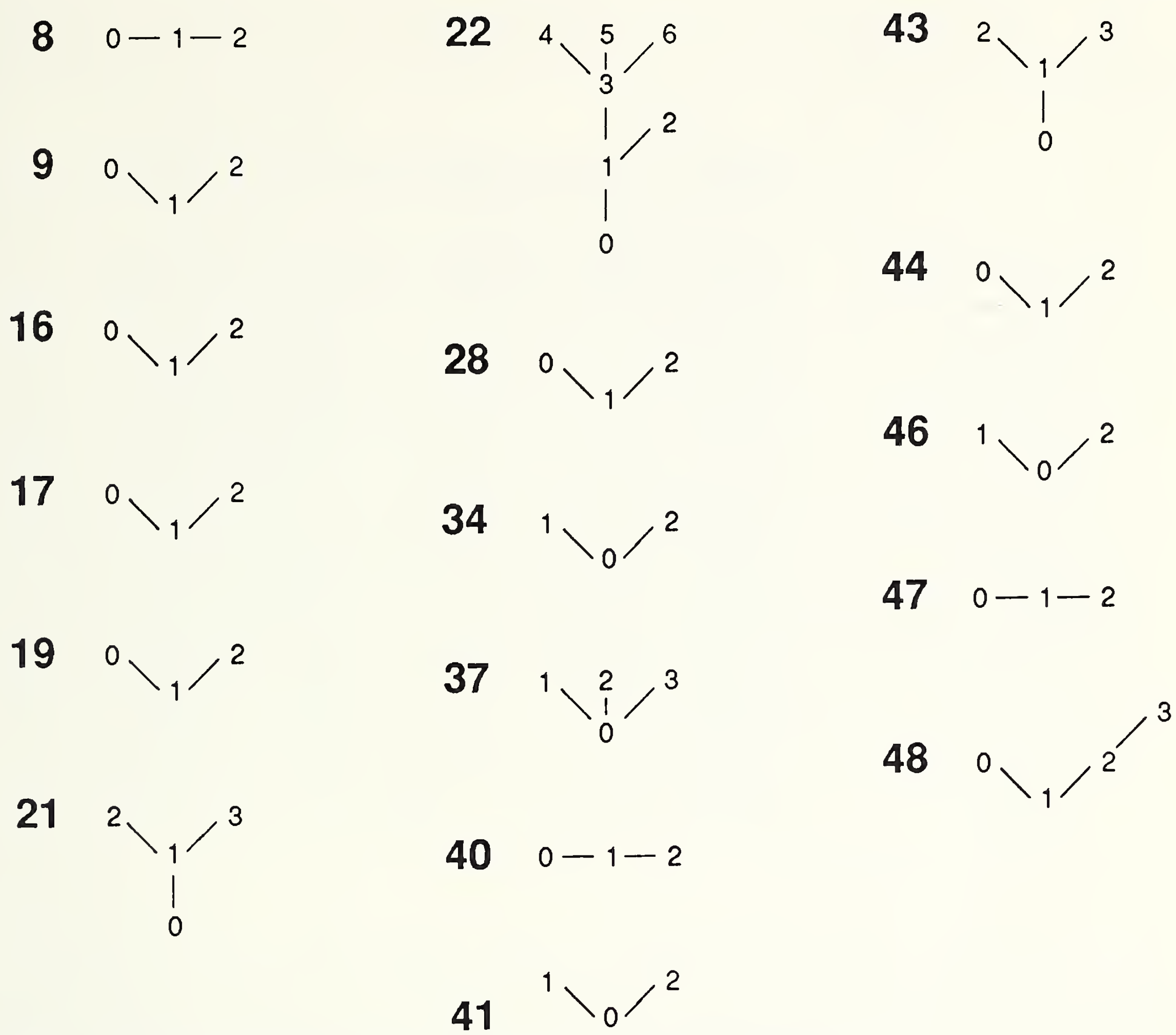


Fig. 2. Character state trees for multistate characters from Table 1.

Topological comparisons. As mentioned above, 2 explicit schemes of relationships have been proposed for the Cimicomorpha, with some additional classifications implying a phylogenetic scheme. Our results—although based on a very different data set—are in agreement with the results of Schuh (1979), in treating the Pachy-

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Fig. 1 Cladogram of Cimicomorpha based on 51 characters described in Table 3, with character states for individual taxa listed in Table 1, and computed from the additively binary coded data in Table 2 (character 18 inactive); length = 156, ci = 49, ri = 68. Characters listed by number and state. The following taxa are autapomorphic for the indicated states: Joppeicidae—5-1, 7-1, 13-1, 20-1, 22-5, 34-0, 41-2, 43-2; Lasiochilidae—37-3; Lyctocoridae—30-1; Medocostidae—3-1, 9-0; Microphysidae—12-1, 21-2, 23-1, 25-1, 42-1, 43-3; Miridae—19-0, 21-2, 22-6, 32-1, 37-1, 43-3; Nabinae—26-0, 28-1, 36-0; Pachynomidae—15-1, 19-1, 29-1, 30-1, 43-3, 48-0; Plokiophilidae—12-1, 34-2, 39-0, 41-2, 43-2, 43-2; Polyctenidae—0-1, 3-1, 6-0, 10-0, 12-1, 17-0, 26-0, 28-1; Prostemmatinae—19-1, 23-0, 40-1, 44-0, 46-0; Reduviidae—11-1, 19-2, 42-1, 48-3; Thaumastocorinae—16-2; Tingidae—3-1, 5-1, 43-2, 49-1; Velocipedidae—15-1, 30-1; Vianaidinae—7-1, 31-1, 43-3.

Table 1. Fifty-one characters used for phylogenetic analysis of Cimicomorpha (see Table 2 for additive binary coding, Table 3 for character descriptions, and Fig. 2 for character state trees).

	0000000000	1111111111	2222222222	3333333333	4444444444	5
	0123456789	0123456789	0123456789	0123456789	0123456789	0
Leptopodomorpha	0000000001	000?001100	0000001000	0011200000	0000101010	0
ancestor	0000000001	10000011- 0	0000000010	000000000-	0002101010	0
Pachynomidae	0000101002	1011110121	0010000021	1000?01000	0203111000	0
Reduviidae	0000101002	1111100122	0010000020	0000201000	0211111030	0
Velocipedidae	0000001001	100?011110	0110000110	1000200001	000110111?	0
Microphysidae	0000000001	1010001200	0231111100	0000100001	0013101110	0
Joppeicidae	1000010101	1001001222	1050101100	0000000001	0202101110	0
Miridae	1000000010	0000001200	0260101100	0011200100	0111101120	0
Xylastodorinae	1011000020	010?001222	0040111000	0001200201	02?3101131	0
Thaumastocorinae	1011000020	010?002222	0040111000	0001200201	0203101131	0
Vianaidinae	1100000110	0001101222	1040?01100	0101200000	011310112?	0
Tingidae s.s.	1101010010	0001101222	1040101100	0001200000	0112101121	0
Medocostidae	0001001000	100?000112	0311001100	1000?01001	00011011??	0
Nabinae	0000001001	1000000112	0311000111	1000110001	0001101110	0
Prostemmatinae	0000001001	1000000111	0310001101	1000111001	1001000110	0
Lasiochilidae	0000001001	1000000100	0320001100	0000?00301	00?11011?0	0
Plokiophilidae	0000001001	1010000100	0320001100	0000200000	12?2202200	0
Lyctocoridae	0000001001	1000000100	0320001100	1000100301	1003202200	0
Anthocoridae	0000001001	1000000100	0320001100	0000100311	2003202200	0
Cimicidae	0100001001	100000010-	0- - - -11100	0000100311	2203202200	1
Polyctenidae	1101000001	001?00000-	0- - - -10110	0000?00311	22?32022- 0	1

nomidae and Reduviidae as sister groups (an idea first proposed by Carayon, 1950a), and treating that group as the sister group of all remaining Cimicomorpha. This scheme argues against the conclusion of Cobben (1968, 1978) that the two groups are not closely related and also offers additional support for placement of the Reduviidae in the Cimicomorpha, contrary to the view of Cobben.

Certain aspects of our results are at variance with those of Kerzhner (1981), however. The main differences are as follows: Kerzhner's placement of the root (Fig. 3) associated the Miridae and Microphysidae with a lineage containing most of the predatory cimicomorphans, whereas in our scheme they belong to a lineage composed of the phytophagous families and the Joppeicidae; he related the Reduviidae and Pachynomidae as sister groups but treated them as being derived from the "Nabidae" (clearly paraphyletic in Kerzhner's sense), whereas in our scheme they are the sister group of all other cimicomorphans; and, the Velocipedidae are placed more basally in our scheme than in his. The other major difference was his treatment of the Anthocoridae *s. l.* as if it were a monophyletic group, and the independent divergence of the Plokiophilidae from the "nabid" lineage prior to the divergence of other cimicoids, whereas according to our analysis the Plokiophilidae belong to the cimicoid lineage.

Character support. The following discussion provides some insight into character support for the various internal nodes of the cladogram (Fig. 1).

Node 1. Elsewhere we have listed the modified sperm storage organs and the micropylar structure of the eggs as synapomorphies for the Cimicomorpha. Our

Table 2. Fifty-one characters used for phylogenetic analysis of Cimicomorpha.

	0000000000111111111 0123456789012345678	1 9	2 0	2 1	2 2	22222223333 34567890123	3 4	33 56	3 7	334 890	4 1	4 2	4 3	4444445 4567890
Leptopod	0000000001000?00110	00	0	000	000000	00010000011	10	00	000	000	00	0	000	1010100
ancestor	000000000110000011-	00	0	000	000000	00000100000	00	00	000	0- 0	00	0	110	1010100
Pachynom	0000101002101111012	01	0	000	100000	00000211000	??	01	000	000	10	0	101	1110000
Reduviid	0000101002111110012	10	0	000	100000	00000200000	10	01	000	000	10	1	100	1110300
Velocipe	0000001001100?01111	00	0	100	100000	00001101000	10	00	000	010	00	0	100	10111?0
Microphy	0000000001101000120	00	0	101	101000	11111000000	01	00	000	010	00	1	101	1011100
Joppeici	1000010101100100122	10	1	000	101001	01011000000	00	00	000	010	10	0	110	1011100
Miridae	1000000010000000120	00	0	101	101100	01011000011	10	00	010	000	01	1	100	1011200
Xylastod	1011000020010?00122	10	0	000	101010	01110000001	10	00	100	010	10	?	101	1011310
Thaumast	1011000020010?00222	10	0	000	101010	01110000001	10	00	100	010	10	0	101	1011310
Vianaidi	1100000110000110122	10	1	000	101010	0?011000101	10	00	000	000	01	1	101	10112?0
Tingidae	1101010010000110122	10	1	000	101010	01011000001	10	00	000	000	01	1	110	1011210
Medocost	0001001000100?00011	10	0	110	100000	10011001000	??	01	000	010	00	0	100	1011??0
Nabinae	0000001001100000011	10	0	110	100000	10001111000	01	10	000	010	00	0	100	1011100
Prostemm	0000001001100000011	01	0	110	100000	00011011000	01	11	000	011	00	0	100	0001100
Lasiochi	0000001001100000010	00	0	110	110000	00011000000	??	00	001	010	00	?	100	1011?00
Plokioph	0000001001101000010	00	0	110	110000	00011000000	10	00	000	001	10	?	110	2022000
Lyctocor	0000001001100000010	00	0	110	110000	00011001000	01	00	001	011	00	0	101	2022000
Anthocor	0000001001100000010	00	0	110	110000	00011000000	01	00	001	112	00	0	101	2022000
Cimicida	0100001001100000010	--	0	---	------	--111000000	01	00	001	112	10	0	101	2022001
Polycten	1101000001001?00000	--	0	---	------	--101100000	??	00	001	112	10	?	101	2022-01

phylogenetic analysis of the group suggests additional synapomorphies. These are: 6-1, presence of the prepedicellite (lost at node 5); and, 10-1, the labium inserted anteriorly on the head (moving to a ventral position at node 7). The presence of the prepedicellite was indicated as possibly synapomorphic for the Cimicomorpha by Zrzavý (1991). The fossula spongiosa (character 16) was thought by Kerzhner (1981) to be synapomorphic for groups contained in our nodes 2 and 11. Other character information in our analysis does not support this interpretation, but rather suggests an independent origin of the fossula spongiosa in the 2 lineages. Characters 22-1 (3–4 cells in the membrane) and 28-1 (spiracles on discrete ventral laterotergites) also support the monophyly of the group, but they show much more variation within the group than the characters mentioned above, and the latter is possibly plesiomorphic, as it occurs widely in the Heteroptera.

Node 2. As indicated in Figure 1, many characters support the monophyly of the Reduviidae + Pachynomidae. Most consistent among these are: 4-1, pedicellar trichobothria; 9-2 structure of the labium; and, 45-1, paired tubular ectodermal pseudospermathecae. Based on their distribution on the cladogram, Brindley's glands (14-1), appear to be of independent origin in the Reduvioidea and Tingidae *s. s.* + Vianaidinae.

Node 3. This previously unrecognized group receives relatively strong support from 3 characters: 21-1, membrane with more than 1 cell and with a stub on the most anterior cell (modified in descendant lineages); 27-1, abdominal spiracle 1 absent (a condition known also in other infraorders); and 47-1, fertilization in lateral oviducts or ovariole pedicels. Only the Reduvioidea (node 2) have retained abdominal spiracle 1 (appearing as a reevolution in the Thaumastocoridae, node 9; see also discussion

Table 3. Characters used in the cladistic analysis of the Cimicomorpha. Left margin: character number, number of steps on tree, consistency index, retention index. All characters active except 18. See Figure 2 for character state trees for multistate characters.

Head				
0	2	50	83	0—dorsum of head capsule usually with 3 pairs of trichobothrium-like setae, 1—dorsum of head capsule without trichobothrium-like setae
1	2	50	66	0—ocelli present, 1—ocelli absent
2	1	100	100	0—mandibular plates of normal size, 1—mandibular plates greatly enlarged and often distinctly surpassing apex of tylus
3	4	25	25	0—buccular bridge present, 1—buccular bridge absent
Antennae				
4	1	100	100	0—pedicel (antennal segment 2) lacking trichobothria, 1—pedicel with between 1 and 20 or more trichobothria
5	2	50	0	0—second antennal segment relatively long, 1—second antennal segment noticeably short
6	3	33	77	0—prepedicellite absent, 1—prepedicellite present
7	2	50	0	0—short, thick, apical seta absent on antennal segment 4, 1—apical seta present on antennal segment 4
Labium				
8	2	100	100	0—labial segment 1 short and not strongly dilated to virtually absent, 1—labial segment 1 long and relatively slender, 2—labial segment 1 short but distinctly dilated
9	3	66	83	0—labium straight, appressed to ventral body surface, segments 3 and 4 relatively long, 1—labium at least weakly curving or angularly bent, flexible, elongate, 2—labium short, stout, strikingly curved, and inflexible
10	3	33	66	0—labium inserted on ventral surface of head, 1—labium inserted anteriorly on head
Thorax				
11	2	50	50	0—stridulatory prosternal sulcus absent, 1—stridulatory prosternal sulcus present
12	4	25	25	0—metathoracic scent gland grooves present on metapleuron, 1—metathoracic scent gland grooves absent or strongly reduced on metapleuron
13	3	33	50	0—metathoracic scent gland with unpaired reservoirs, 1—metathoracic scent gland with paired reservoirs
14	2	50	66	0—Brindley's gland absent, 1—Brindley's gland present
Abdominal Trichobothria				
15	2	50	0	0—abdominal trichobothria absent, 1—abdominal venter with a trichobothrium either side of midline on segments 3–7
Legs				
16	3	66	88	0—fossula spongiosa present (at least vestigially) apicoventrally on at least foretibiae, clothed with modified microtrichia, 1—fossula spongiosa absent, 2—tibial appendix present on membrane at apex of tibia, clothed with unmodified hairs
17	2	100	100	0—tarsi 4 segmented, 1—tarsi 3 segmented, 2—tarsi 2 segmented
18 [Inactive]				0—metacoxae cardinate, 1—metacoxae intermediate, 2—metacoxae rotatory

Table 3. Continued.

Wings				
19	6	33	21	0—costal fracture long, delimiting cuneus, 1—costal fracture short, interrupting costal margin of wing, not delimiting a distinct cuneus, 2—costal fracture absent
20	2	50	50	0—R + M in forewing not raised and keel-like, 1—R + M in forewing raised and keel-like
21	4	75	96	0—membrane without a stub, 1—membrane with more than one cell and with a stub on the most anterior cell, 2—membrane with a stub on distal angle of a single cell or pair of cells, 3—membrane with a stub on a vein diverging from corium–membrane boundary or as a separate bulge
22	7	86	94	0—membrane with 4 or 5 long closed cells and no emanating veins, 1—membrane with 3–4 short to long cells (sometimes not closed), not attached to cuneal region, usually with many emanating free veins, or 2 or 3 usually long (rarely short) cells not attached to cuneal region (rarely not closed), and usually with only a few to no free veins emanating from them, and sometimes with one free posterior vein (sometimes branched), 2—membrane with 4–5 free veins, rarely with 1 long closed cell with no emanating veins, 3—membrane with 1 small, strongly sclerotized cell not attached to cuneal region, with a few indistinct emanating veins (with a stub), 4—membrane with no cells (and no stub), either no veins or veins percurrent from corial area not differentiated from membrane, 5—membrane with a short transverse cell and a few free emanating veins (no stub), 6—membrane with 1 or 2 short cells (if 2, the anterior one attached to cuneus), rarely with a few emanating vein-like structures, and with one posterior free vein; stub present on distal angle of cell or cells
23	3	33	0	0—distal sector of R + M in hindwing not branching, 1—distal sector of R + M branching
24	1	100	100	0—m-cu crossvein present in hind wing, 1—m-cu crossvein absent in hindwing
Abdomen				
25	3	33	50	0—dorsal laterotergites not fused with mediotergites, 1—dorsal laterotergites fused with mediotergites
26	4	25	40	0—ventral laterotergites visible and not fused with abdominal sternum, 1—ventral laterotergites not visible and fused with abdominal sternum
27	2	50	80	0—abdominal spiracle 1 present, 1—abdominal spiracle 1 absent
28	5	40	50	0—spiracles on ventral plate formed by fusion of sternum and ventral laterotergite, 1—spiracles on discrete ventral laterotergite, 2—spiracles on sternum adjacent to discrete ventral laterotergite
29	2	50	50	0—fossettes parastigmatiques absent, 1—fossettes parastigmatiques present
30	4	25	40	0—apophysis absent internally on abdominal sternum 7 in female, 1—apophysis present internally on abdominal sternum 7 in female
31	1	100	100	0—scent gland present between abdominal terga 3 and 4 in larvae, 1—scent gland absent between abdominal terga 3 and 4 in larvae
32	2	50	0	0—scent gland present between abdominal terga 4 and 5 in larvae, 1—scent gland absent between abdominal terga 4 and 5 in larvae
33	2	50	80	0—scent gland present between abdominal terga 5 and 6 in larvae, 1—scent gland absent between abdominal terga 5 and 6 in larvae

Table 3. Continued.

34	7	28	37	0—scent gland present between abdominal terga 6 and 7 in larvae, 1—scent gland scar present between abdominal terga 6 and 7 in larvae, 2—scent gland absent between abdominal terga 6 and 7 in larvae
35	1	100	100	0—Ekblom's organ absent, 1—Ekblom's organ present
36	3	33	33	0—male abdominal segment 8 normally developed and exposed, 1—male abdominal segment 8 reduced and for the most part telescoped within segment 7
Genitalia and Insemination				
37	4	73	92	0—male terminalia symmetrical, 1—male terminalia asymmetrical, mirid type, 2—male terminalia asymmetrical, thaumastocorid type, 3—male terminalia asymmetrical, cimicoid type
38	1	100	100	0—male with noncopulatory paramere, 1—left paramere of male modified into a copulatory organ
39	3	33	66	0—general direction of parameres usually backwards, 1—general direction of parameres forward
40	3	66	85	0—distal portion of phallus in male neither with acus nor situated within paramere, 1—vesica in male with acus, 2—vesica in male membranous and incorporated into paramere
41	6	33	71	0—ovipositor laciniate, valvula I (= gonapophysis I) associated by ramus with valvifer I (= gonocoxite I), 1—ovipositor laciniate, but connection of valvula I with valvifer I lost, 2—ovipositor platelike to reduced
42	3	33	50	0—ventral laterotergite 8 in female free of valvifer I (= gonocoxite I) or incompletely fused with the latter, 1—ventral laterotergite 8 in female fully fused with valvifer I
43	10	30	50	0—spermatheca present and functional, 1—spermatheca transformed into form of a vermiform gland, 2—spermatheca reduced and nonfunctional, 3—spermatheca absent
44	2	100	100	0—spermatolytic nonsyncitial bodies present, 1—spermatolytic bodies absent, 2—spermatolytic syncitial bodies present
45	1	100	100	0—paired ectodermal tubular pseudospermathecae absent, or analogous structures saclike, 1—paired ectodermal tubular pseudospermathecae situated on medial ectodermal portion of female gonoducts
46	2	100	100	0—haemocoelic insemination via puncture of vaginal wall, 1—insemination via normal gonoducts, 2—hemocoelic insemination via puncture of abdominal wall or metacoxal membrane
47	2	100	100	0—fertilization in ectodermal parts of reproductive system, 1—fertilization in lateral oviducts or ovarial pedicels, 2—fertilization in vitellarium
Eggs				
48	6	50	72	0—eggs with no micropyles, 1—eggs with 1 micropyle, 2—eggs with 2 micropyles, 3—eggs with 3 or more micropyles
Habits				
49	2	50	100	0—predaceous, 1—phytophagous
50	1	100	100	0—free living, not feeding on vertebrate blood, 1—ectoparasitic, feeding on vertebrate blood

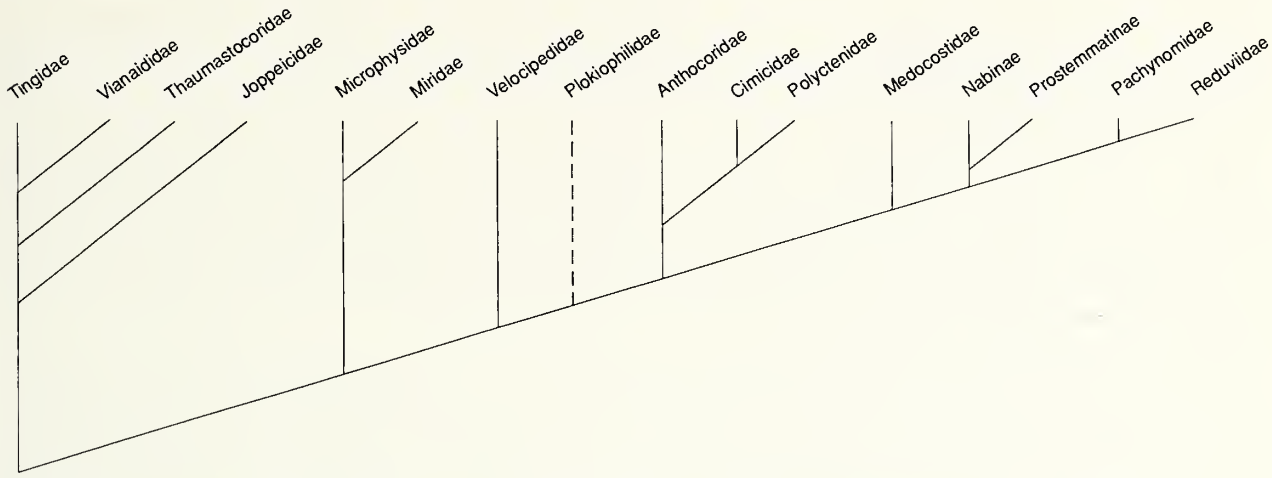

Fig. 3. Kerzhner's (1981) cladogram of the Cimicomorpha (redrawn).

of character 27 in the Appendix). Also, only the Reduvioidea retain the plesiomorphic site of fertilization in the ectodermal portions of the female gonoducts, even after the loss of the true spermatheca. In other cimicomorphans, regardless of the method of insemination or in what type of organs (ectodermal or mesodermal origin) the sperm is stored, fertilization always occurs in the mesodermal portions of the female gonoducts or even in the vitellarium, as documented or inferred from anatomical structure in numerous papers by Carayon (e.g., 1954, 1977a).

Velocipedidae. The absence of the fossula spongiosa in this apparently predatory group is something of an enigma to us. Nonetheless, close examination of a number of species, with both males and females represented, revealed no evidence of the structure.

Node 4. This grouping receives its strongest support from characters 26-1, the fusion of the ventral laterotergites with the sternal plate (ventral laterotergites being present only in the Nabinae and Polyctenidae, and possibly indicated in the Prostemmatinae: Phorticini) and 28-0, the location of spiracles 2-8 on that plate (excluding the above mentioned taxa). Both attributes show considerable variation within the

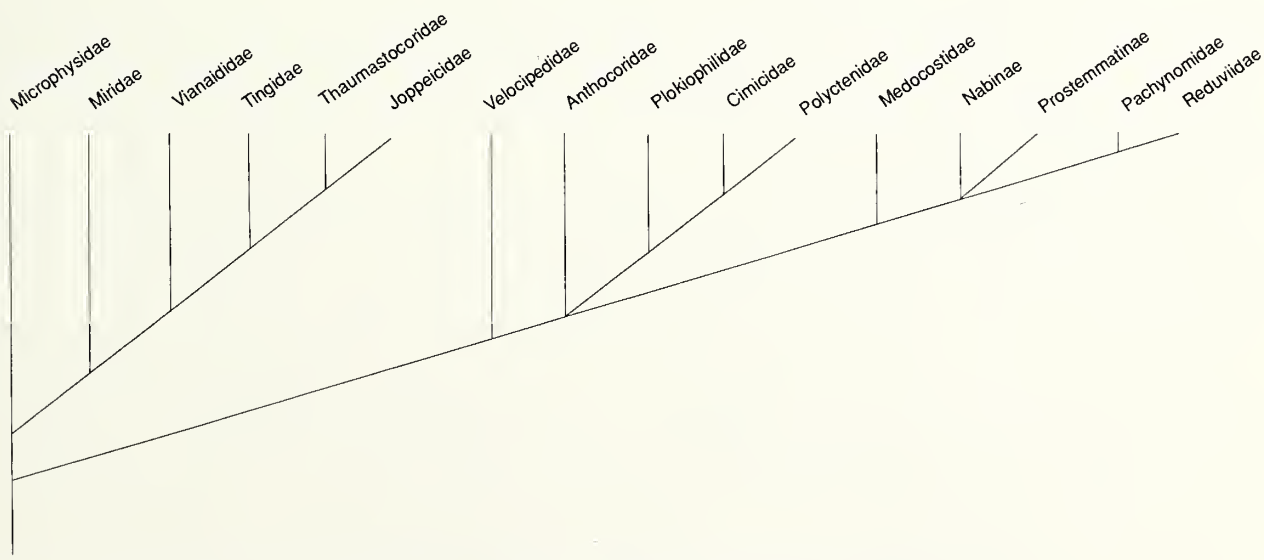

Fig. 4. Most parsimonious cladogram based on Kerzhner's (1981) data.

Heteroptera, but are highly consistent within the Cimicomorpha. Character 34-1, presence of scent gland scars on larval abdominal segments 6–7 is probably a remnant of a once present gland.

Node 5. The loss or reduction of a number of features serve to characterize this lineage. These include: absence of the prepedicellite (6-0); reduction of number of cells in the membrane (22, several states); and, absence of m-cu in hind wing (24-1). All members of the clade except most Miridae have 2-segmented tarsi (17-2) (see Character Discussion below).

Node 6. Inclusion of the Joppeicidae at this node is somewhat problematic, in that it possesses mostly autapomorphies as well as having certain primitive characteristics (e.g., retention of spermatheca, larval gland 6/7) that do not occur in the remaining members of this lineage. Nonetheless, lack of cephalic trichobothria (0-1), absence of the costal fracture (19-2), and absence of the stub on the membrane (21-0) argue for the monophyly of the group (see Character Discussion below).

Node 7. This node groups together those families of Cimicomorpha most of whose members are phytophagous. They all have a labium of similar structure to that found in the Pentatomomorpha (8-1, 9-0, 10-0) (which has been further modified in the Thaumastocoridae in a way also found in some Dipsocoromorpha), but our analysis suggests clearly that the similarity of structure in the labium in these last two groups is the result of convergence. There is also considerable consistency in the absence of larval scent glands between abdominal segments 5-6 and 6-7 (33-1, 34-2) and presence of 2 micropyles on the egg (48-2; secondarily modified in the Thaumastocoridae).

Node 8. Although the two subgroups of Thaumastocoridae recognized here have been associated with one another by most modern authors (a grouping with substantial character support in our analysis), their position within the Heteroptera, and more specifically, the Cimicomorpha, has been thought problematic in the minds of some authors (e.g., Cobben, 1978). Nonetheless, as noted above, there are a number of characters which unite the Thaumastocoridae with the Miroidea of Drake and Davis (1960). The thaumastocorid micropylar type was found to be unique by Cobben (1968), but nevertheless appears to be derived from the mirid-tingid type (2 micropyles) as already noted. The phylogenetic analysis suggests the tibial appendix found in the Thaumastocorinae (character 16-2) is not homologous with the fossula spongiosa of other cimicomorphans, and we have so coded it.

Node 9. The Miridae have been associated with the Tingidae *s. l.* by some authors (e.g., Drake and Davis, 1960). Although both groups have many characters unique to them, there is support for a sister group relationship, particularly in the structure of the ovipositor (41-1; 42-1).

Miridae. Among those characters listed in the caption to Figure 1 as diagnostic for the Miridae, the cladogram suggests that several have arisen secondarily. The presence of 1 or 2 cells in the membrane (22-6) appears to be derived from the condition of having no cells. The stub (21-2), which is readily observed on the distal angle of the cells in many Miridae, like the membrane venation itself, appears to have arisen from the stubless condition; the stub is present elsewhere in the Miriformes only in the Microphysidae. The Miridae are coded as having 2-segmented tarsi (17-2), because many of its most primitive members—Isometopinae, Psallopinae, some Cylapinae—have that condition, whereas the majority of all others have 3-segmented tarsi. See also Character Discussion below.

Node 10. The Tingidae *s. s.* and Vianaidinae appear as sister groups in our analysis, which is in agreement with the conclusions Drake and Davis (1960) and Carayon (1962b). Character state 14-1, presence of Brindley's glands, shared with the Reduvioidea, suggests that the similar appearing structures in the two groups are not homologous.

Node 11. This grouping of Medocostidae + Nabidae + Cimicoidea is supported by the presence of the fossula spongiosa (16-0) and the distinctive structure and location of the stub (21-3). We assume that in the Velocipedidae and Microphysidae the stub has remained associated with a cell on the membrane, while it has been transferred onto the vein forming the corium–membrane boundary in the taxa grouped under this node. Carayon (1950a, and elsewhere), on the basis of anatomical characters, noted what he believed to be a close relationship between the Nabidae and Cimicoidea *s. s.* as opposed to a relationship between the Nabidae and Reduviidae. Clearly, our results support his contention.

Node 12. Character 19 (condition of the costal fracture), 23-1 (distal sector of R+M branching), and 30-1 (internal apophysis on abdominal segment 7 of female) all are variable within this group and/or occur in other cimicomorphan taxa. They nonetheless support a close relationship among these 3 groups. Carayon (1970) and Kerzhner (1981) included the Medocostidae (and Velocipedidae) within the Nabidae. Kerzhner (1981) supported this by 3 "synapomorphies," viz., 1) presence of the fossula spongiosa (a synapomorphy of the Cimiciformes), 2) loss of live veins on the membrane jointly with the presence of a "stub" (actually synapomorphic at node 11, including also the Cimicoidea), and 3) presence of taenidia (sclerotized supporting rings) in the seminal duct between the basal apparatus of the phallus and the endosoma (Carayon, 1970: fig. 29; Kerzhner, 1981: figs. 59v, 63). Only the last character may be synapomorphic for node 12, but there is no comprehensive comparative morphological study available and we have therefore not included it in our analysis. In view of the relatively weak character support for this grouping we follow Štys (1967a) and treat *Medocostes* as belonging to a distinct family.

Node 13. The two subgroups of Nabidae (with their rather different facies) are held together by their possession of fossettes parastigmatiques (29-1) and Ekblom's organ (35-1), the former attribute also apparently occurring in the Pachynomidae, although our analysis suggests that the structure in that family is of a different origin based on its distribution in our cladogram.

Node 14. Although the facies of taxa included at this node are quite similar (with the exception of the Polyctenidae), character support is somewhat ambiguous because of the variant membrane venation (character 22) and the essentially symmetrical male genitalia in the Plokiophilidae. In our view, the simplest explanation is that the form of the left paramere (37-3) in the Lasiochilidae is not homologous with that found in the Lyctocoridae, Anthocoridae, Cimicidae, and Polyctenidae. Certainly, our analysis strongly suggests asymmetrical male genitalia have arisen several times in the Cimicomorpha.

Node 15. The studies of Carayon, as synthesized by Ford (ms) offer strong support for the taxa included at this node from characters in the male and female genitalia and reproductive systems and the eggs (40-1, 43-2, 44-2, 46-2, 47-2, 48-0).

Node 16. The asymmetrical male genitalia (37-3), and spermatheca absent (43-3) suggest that all taxa at node 16 form a monophyletic group.

Node 17. The structure of the left paramere, in the form of a copulatory organ (38-1) and the membranous vesica incorporated into that paramere (40-2) support grouping the Anthocoridae, Cimicidae, and Polyctenidae. The relationships of the Cimicidae are strongly suggested as with the Xylocorini; however, the Polyctenidae, with their grossly modified structure, assume a much less clear-cut position, outside of the fact that their male and female genitalia clearly associate them with the Anthocoridae and Cimicidae.

Node 18. Although 4 attributes indicate that the Cimicidae + Polyctenidae form a monophyletic unit, we place little credence in this result. The Polyctenidae possesses some seemingly plesiomorphic characters (such as distinct ventral laterotergites [26-0, 28-1]; well developed first labial segment; and presence of the first abdominal sternum, a feature unique in the Cimicomorpha). We regard these attributes as reversals or possibly associated with a neotenous nature of this family; the method of traumatic insemination in the Polyctenidae differs from that of the other cimicoid families and has been regarded by Carayon (1977a) as plesiomorphic.

DISCUSSION OF SELECTED CHARACTERS

Ocelli. Absence of ocelli is often associated with brachyptery in the Heteroptera. Even though certain families lack ocelli on a consistent basis (Tingidae, most Miridae, Pyrrhocoridae, Largidae, and most nepomorphan families), occasionally ocelli are absent in genera perfectly capable of flight, but which nonetheless belong to families which almost consistently possess the organs (e.g., *Camptocera* and *Lipostemmata* in the rhyparochromine Lygaeidae). The loss of ocelli in the Cimicomorpha is a synapomorphy uniting the Tingidae *s. s.* with the Vianaidinae, and the Cimicidae with the Polyctenidae (a grouping of doubtful validity, none of whose members can fly). Ocelli are occasionally lacking in some members of other families such as Reduviidae, Anthocoridae, and female Microphysidae, but consistently only in the Miridae other than the Isometopinae. Thus, the loss of ocelli appears to be a character of little phylogenetic significance, at least within the Cimicomorpha, though their independent loss in the Tingidae and non-isometopine Miridae is noteworthy, and we find no evidence to suggest that those groups, *inter se,* are not monophyletic.

Labial segmentation. Discussions in the literature about the labium have revolved primarily around whether or not segment 1 is present or not. Our observations and analysis suggest that much of such discussion is irrelevant because the degree of development in segment 1 is highly variable even within individual families in the Cimicomorpha. For example, it is greatly reduced to absent in most, but not all Reduviidae, and in many, but by no means all, Cimicoidea (e.g., present in the Polyctenidae). The more fundamental distinction seems to be whether labial segment 1 takes on a form similar to that found in the Miridae and other predominantly phytophagous lineages (elongate and somewhat flared distally), or whether it is of the form found in the predators (usually relatively short to almost absent and of nearly uniform diameter over its entire length). Variation similar to that found in the Cimicomorpha is also found in the Leptopodomorpha, and indeed other higher groups such as the Dipsocoromorpha and Nepomorpha show substantial variation in labial length and the proportional lengths of the segments.

Costal fracture. The absence or presence (and degree of development) of the costal fracture is problematic in that no matter how the transformation stages are coded, the character is always homoplasious on the cladogram. We have regarded the long costal fracture as plesiomorphic in the Cimicomorpha because it is usually long in the Saldidae. The costal fracture is present in this condition in some Pachynomidae (a short fracture being an apparent reduction), Velocipedidae, Microphysidae, and Cimicoidea, but is lost elsewhere, notably in the Reduviidae, and groups contained in nodes 6 (Joppeicidae and Miroidea) and 12 (Naboidea) of Figure 1. However, the costal fracture must be re-evolved in the Miridae (as a long fracture which has been independently lost in a few genera) and Prostemmatinae, respectively. Two less parsimonious explanations are that the presence of the costal fracture always represents a primitive condition and that losses are more frequent than suggested on the cladogram; or, that the costal fracture is a character not belonging to the cimicomorphan (and possibly heteropteran) ground plan, and that it has evolved independently in all of those groups that possess it. It appears that a re-examination of the homology of the costal fracture in the entire Heteroptera will be necessary to further clarify the situation.

Membrane venation and stub. Kerzhner's treatment of the Reduvioidea as closely related to the Nabinae and Prostemmatinae, derived largely from his view that the membrane venation in these groups consists only of "dead" veins. In our earliest attempts at coding characters of wing venation, we accepted Kerzhner's theory of evolution of veins in the membrane exactly as he presented it. This interpretation yielded results in which attributes of membrane venation were not congruent with other characters. We therefore reexamined and recoded characters pertaining to membrane venation, treating cell forming veins as homologous (Table 1, character 22), an approach which produced a much more stable result and much greater character congruence. Our parsimony analysis suggests that the membrane venation has arisen *de novo* in the Miridae after having been lost at node 6 in Figure 1.

The stub (coded as character 21, separately from the free and cell forming veins of the membrane) emerged from our analysis as an important group defining character, although it previously had been incorporated in systematic studies of the Heteroptera only by Kerzhner (1981). The pattern of occurence of the stub is most complicated in the Miriformes and follows a pattern of occurence identical to that of the membrane veins themselves. Our parsimony analysis suggests that the stub is in the ground plan of that group and that it has reevolved in the Miridae. We suggest that additional enquiry will probably support the theory of multiple loss, because the absence of the stub within the Miriformes is restricted to those groups in which membrane venation is greatly reduced or completely wanting, viz., Joppeicidae, Thaumastocoridae, and Tingidae *s. l.*

Fossula spongiosa. Kerzhner (1981) treated the fossula spongiosa, a character unique to the Cimicomorpha, as a synapomorphy for the Reduvioidea and taxa contained in our node 11. Our parsimony analysis suggests that the structure has evolved independently in the Reduvioidea and Cimiciformes, rather than having been lost twice independently (in the Velocipedidae and the taxa contained in node 5) as would be required if it were interpreted as synapomorphic for the Cimicomorpha on the cladogram in Figure 1. Detailed morphological comparison of the fine structure of the fossula spongiosa in the Reduvioidea and the Cimiciformes should be conducted

to provide additional information supporting one of these alternatives.[1] The tibial appendix in the Thaumastocorinae seems rather obviously to be an organ developed *de novo* and not homologous with the fossula spongiosa found in other cimicomorphans.

Tarsal segmentation. The literature on the Cimicomorpha is filled with arguments concerning whether number of tarsal segments is diagnostic for higher taxa or placement of various "annectant" genera. Reading such comments one might conclude that reduced tarsal segmentation is simply an autapomorphous condition in a few families. However, our analysis supports the idea of 2-segmented tarsi as a synapomorphy for a large clade (node 5), with substantial support from other characters. Not only might this result render much previous discussion moot, but it also has implications for the condition of the tarsus in the Miridae. If, as is generally assumed, the Isometopinae are the sister group of all other Miridae, then the 2-segmented tarsi may be part of the ground plan of the group. Indeed, several apparently primitive non-isometopine genera of Miridae, e.g., *Peritropis* Uhler and *Psallops* Usinger also have 2-segmented tarsi.

Abdominal spiracle 1. The first abdominal spiracle appears to have been re-evolved in the Thaumastocoridae, based on the position of the group on the cladogram, and the fact that the structure occurs elsewhere in the Cimicomorpha only in the Reduvioidea. To assume that abdominal spiracle 1 has been retained in the thaumastocorids would require losing it 5 times independently in other taxa. We might assume that in the stem group for node 3 the genetic information regulating the development of the spiracle has been blocked, but never fully lost.

Vermiform gland. Kerzhner's (1981) placement of the root in his cladogram was based strongly on the presumption that the possession of a vermiform gland (character 43-1) is synapomorphic for cimicomorphans that possess the structure (and those which apparently have lost it secondarily, i.e., Pachynomidae, Microphysidae, and most Cimicoidea). Our interpretation suggests rather that the vermiform gland is synapomorphic for all Cimicomorpha and that it has been modified or lost in all groups that do not possess it. What seems clear is that our understanding of homology with regard to transformation of the functional spermatheca is in need of further

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[1] Three attributes, the fossula spongiosa, stub on the forewing membrane, and general venation of the forewing membrane, all appear to be independently evolved in 2 cimicomorphan lineages– at least according to our parsimony analysis. This result exists in spite of the fact that we have coded all characters in such a way as to show maximum congruence on the cladogram—at least within the limits of our ability to understand homology. The multiple evolution of complex structures has been deemed by many authors a less satisfactory explanation of character evolution than multiple loss, even though one or more additional steps may be required on the cladogram. In the case of the three attributes mentioned above, we are also inclined towards multiple loss as the preferred explanation, by virtue of the fact that relatively complex characters need not appear more than once in an apparently identical form. Nonetheless, other factors, such as a sample for the Joppeicidae with no variation, may influence our ability to correctly determine homology; indeed the Joppeicidae are one of the most difficult groups to place (have the relatively weakest character support) in our scheme. Detailed structural analysis may help to determine whether all of our homology statements are correct. Corroboration or rejection of the phylogenetic theory presented in Figure 1 will require additional character information, possibly from molecular data.

study in the Cimicomorpha. Particularly puzzling is the occurrence of a "vestigial" spermatheca not transformed into a vermiform gland in such distantly related groups as Joppeicidae, Tingidae (Cantacaderinae), and Plokiophilidae, all the more so when one notes that these groups are placed relatively high on the cladogram.

Some other striking similarities of apparently independent origin might be mentioned, as for example the presence of Brindley's glands in the Reduvioidea and Tingidae. However striking some of these resemblances, they represent only homoplasies in individual characters, and more thorough morphological and developmental investigations could (and should, if we are right), reveal that similarities in these and other cases are superficial rather than the result of homology.

CLASSIFICATION OF THE CIMICOMORPHA

The last well documented effort at a comprehensive suprafamilial classification of the Cimicomorpha was that of Reuter (1910); yet, his effort now has many limitations, because of a revised diagnosis and consequent altered composition of the group. Štys and Kerzhner (1975) provided a formal classification of superfamilies, but without character documentation; we do not attempt here to list or discuss all of the diverse superfamilial concepts that exist in the literature. Schuh (1986) listed only two higher categories that could be recognized more or less consistently: Reduvioidea and Cimicoidea *s. s.*, with all other families being treated as *incertae sedis.* Carayon (1977a, b, 1984) and Péricart (1983) recognized the Reduvioidea and Cimicoidea, the latter taxon including all non-reduvioid cimicomorphans. Carayon subdivided his very broadly conceived Cimicoidea into two series, Miriformes and Cimiciformes (names proposed by Reuter [1910], for groups of a somewhat different conception); these two groups correspond to clades recognized in our analysis, with the exception of the Velocipedidae and Thaumastocoridae, and we have therefore recognized them in the following formal sequenced classification (Nelson, 1973):

Cimicomorpha
- Reduvioidea
  - Pachynomidae
  - Reduviidae
- Velocipedoidea
  - Velocipedidae
- Miriformes
  - Microphysoidea
    - Microphysidae
  - Joppeicoidea
    - Joppeicidae
  - Miroidea
    - Thaumastocoridae
    - Miridae
    - Tingidae
- Cimiciformes
  - Naboidea
    - Medocostidae
    - Nabidae

Cimicoidea
- Lasiochilidae
- Plokiophilidae
- Lyctocoridae
- Anthocoridae
- Cimicidae
- Polyctenidae

The Reduvioidea have been recognized by many authors, and our analysis supports the group as well founded. We continue the formal use of this name.

The lineage including the Velocipedidae and all remaining Cimicomorpha has been recognized explicitly by Péricart (1983) and implicitly by Carayon (1977a, b, 1984). We emphasize that the inclusion of the Velocipedidae in the Nabidae, as done by several modern authors (Carayon, 1970; Kerzhner, 1971, 1981) obscures the true relationships of the group. Kerzhner (1981) found support for his admitted paraphyletic and broadly conceived Nabidae (including Velocipedidae and Medocostidae) in an essentially similar phallus (all elements of the basal apparatus fused in a ring, the latter fused with the proximally membranous phallotheca, and the endosoma membranous and not subdivided into a conjunctiva and vesica). This type of phallus may actually be synapomorphic for all Cimicomorpha, or at least non-reduvioid cimicomorphans, and in the absence of a more detailed comparative study, we cannot accept it as merely a "nabid" synapomorphy. Although Kerzhner's (1981) classification of the Nabidae is not accepted here, he clearly recognized the relatively primitive phylogenetic position of the Velocipedidae within the Cimicomorpha, as can be seen in his cladogram. We place the family in a distinct superfamily, Velocipedoidea.

For the microphysid-mirid lineage, we use the existing name Miriformes as applied by Carayon. Classical authors, such as Reuter and McAtee and Malloch, often included the Microphysidae within the Anthocoridae *s. l.* When the Plokiophilidae were first discovered they were placed in the Microphysidae because the known members had two-segmented tarsi. Improved knowledge of genitalic structure in the true cimicoids and the Microphysidae made it clear that no such close relationships existed. A relationship between the Microphysidae and Miridae has been suggested by some authors (e.g., China, 1933, 1955; Štys, 1962; Kerzhner, 1981), and our results suggest that this theory has merit over the microphysid-cimicoid theory. We place the Microphysidae within the superfamily Microphysoidea, to our knowledge for the first time.

The position of the Joppeicidae has always been the subject of dispute. The group has many unique characters, and is placed in the Miriformes with difficulty because of the structure of the labium and its insertion anteriorly on the head. Davis and Usinger (1970) suggested that *Joppeicus* was related to the Tingidae, a similar position being advocated by Kerzhner (1981). Likewise, Carayon (1977a, b, 1984) and Péricart (1983) explicitly related the Joppeicidae to the Tingidae, including also the Miridae and Microphysidae, but made no mention of the Thaumastocoridae. We treat the Joppeicidae as the single family within the Joppeicoidea, as already done by Štys and Kerzhner (1975).

Drake and Davis (1960) used the name Miroidea to include the Tingidae *s. l.* and

the Miridae. Our results support their theory, including the treatment of the Vianaidinae as a subfamily of the Tingidae. However, we use Miroidea in a broader sense, to include also the Thaumastocoridae.

For the nabid–cimicoid lineage we use name Cimiciformes as construed by Carayon (1977a, b, 1984), but excluding the Velocipedidae. We recognize two superfamilies, Naboidea and Cimicoidea *s. s.*

Naboidea. We recognize the Nabidae as including only the Nabinae and Prostemmatinae. The Medocostidae, sometimes included in the Nabidae (e.g., Kerzhner, 1981), always grouped with the Nabidae in our analyses, but because of the unusual combination of attributes, we treat the group as a distinct family.

Cimicoidea. We use this term in the sense of Ford (ms), to include only the Plokiophilidae, Cimicidae, Polyctenidae, and those taxa placed in the traditional Anthocoridae (Lasiochilidae, Lyctocoridae, and Anthocoridae *s. s.*).

In preparing the present classification of the Cimicomorpha the following taxa presented the question of appropriate rank: Isometopinae + Miridae; Thaumastocorinae + Xylastodorinae; Nabinae + Prostemmatinae; Cimicidae + Anthocoridae; and Phymatinae (and related subfamilies) + Reduviidae.

Unfortunately, the process of classification offers no obvious rules for determining the ranks of taxa. At a minimum we recognized monophyletic groups. Beyond that, we have grouped at the family level units which are monophyletic and also satisfied one or more of the following criteria: the rank was in accord with that assigned by recent authorities in the group; the range of morphological variation was less within the group than between it and its sister group; long recognized nomenclature was retained while still satisfying other criteria; and the taxon had been traditionally recognized.

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APPENDIX

EXPLANATION OF CHARACTERS AND DISCUSSION OF THEIR INTERPRETATION

Head

0. Cephalic trichobothria are widely distributed in the Heteroptera, and appear to be part of the ground plan for the order, at least at the level of Euheteroptera and possibly also including Enicocephalomorpha. Andersen (1982) proposed the deep pitlike bothrium as a synapomorphy in the Gerromorpha. In non-gerromorphan Heteroptera there is often little difference other than length and constant position to distinguish the trichobothrium-like setae from many other setae on the head, but their loss in many groups has been interpreted as a synapomorphy by Kerzhner (1981), and when treated as such does seem to be congruent with the distribution of other characters in the Cimicomorpha (see also Schuh, 1979). Not all members of those groups for which cephalic trichobothria are indicated as present actually have the structures, and some taxa for which they are indicated as lost, appear to possess them.

1. Ocelli are coded as present in the Miridae because of their existence in the Isometopinae, the putative sister group of all other Miridae (Schuh, 1974, 1976).

2. We adopt the term mandibular plate (=juga, paraclypeus) in accordance with current morphological usage. In most cimicomorphans this structure is normally developed, whereas it is generally enlarged in the Thaumastocorinae and Xylastodorinae (see figures in Drake and Slater [1957], and Slater and Schuh [1990]).

3. The buccular bridge is a transverse rampartlike structure formed by the bucculae, situated at the anterior margin of the gula and caudad of the base of the labium. It occurs in most predaceous Heteroptera, but it is often absent in phytophagous groups with long bucculae. The structure has been recognized, and its distribution in the

Cimicomorpha checked, by Štys (unpubl.) during his comparative study of the *Medocostes.* Presence or absence of the buccular bridge was used as a character by Kerzhner (1981). We have done additional checking for the structure in the Thaumastocorinae (absent with the possible exception of *Thaumastocoris*), Xylastodorinae (absent), and Polyctenidae (absent), and Vianaidinae (present).

Antenna

4. Lent and Wygodzinsky (1979) documented the occurrence of pedicellar trichobothria in the antennae of Triatominae (Reduviidae). Wygodzinsky and Lodhi (1990) provided detailed information of their distribution in most reduviid subgroups as well as in the Pachynomidae. We note that a few members of these groups do not possess the structures. Zrzavý (1990) summarized the occurrence of antennal trichobothria in all Heteroptera.

5. Kerzhner (1981) recognized two character states relative to the length of antennal segments 1 and 2: segments 1 and 2 short, or at least segment 2 long. Our analysis suggests that the actual character information concerns the length of segment 2. A short second segment is always combined with a short first segment in Joppeicidae and in most Tingidae *s. s.,* although some Tinginae may have a very long first segment. Contrary to Kerzhner, segment 2 is always long in the Thaumastocorinae and in *Xylastodoris*; only in *Discocoris* (Xylastodorinae), is segment 2 very short. Thus, we coded both Thaumastocorinae and Xylastodorinae as having segment 2 long, as this appears to be the ground plan condition.

6. The distribution of the prepedicellite is based on the work of Zrzavý (1991). The prepedicellite is a secondary segment formed by the separation of the base of the pedicel; it is usually small and ringlike, but sometimes conspicuously long, as in the Prostemmatinae. Some families exhibit some degree of variation; of those coded as lacking the prepedicellite some Miridae (Termatophylini) possess it, while of those coded as having the structure, it is actually absent in many Cimicidae (Cimicinae) and Reduviidae.

7. The distribution of the apical antennal seta is based on the work of Zrzavý (1991).

Labium

8. The first labial segment is truly elongate in the Tingidae *s. s.,* Vianaidinae, and Miridae only (Fig. 5F); it is abbreviated and distinctly dilated in the Thaumastocoridae and Xylastodorinae (less strongly so in *Xylastodoris*) (Drake and Slater, 1957: fig. 7), in a manner similar to that found in many Schizopteridae. In all other families of Cimicomorpha labial segment 1 is noticeably abbreviated (Fig. 5D), and in some taxa hidden between the bucculae (Fig. 5G), or it may be reduced to a ring or be virtually absent (Fig. 5E); we have combined all of these conditions under state 1 because many transitional conditions occur and because the situation in some families is quite diverse. Labial segment 1 is well developed in the Palearctic genera of Microphysidae, but strongly abbreviated in the American genera of the family. It is well developed and externally easily visible in the Nabinae, Prostemmatinae, Pachynomidae, and Reduviidae, Centrocneminae (Miller, 1955, 1956a). It is strongly abbreviated and hidden between the bucculae in the Velocipedidae and Medocostidae, and is reduced to a ring or virtually absent in the other Reduviidae, Joppeicidae,

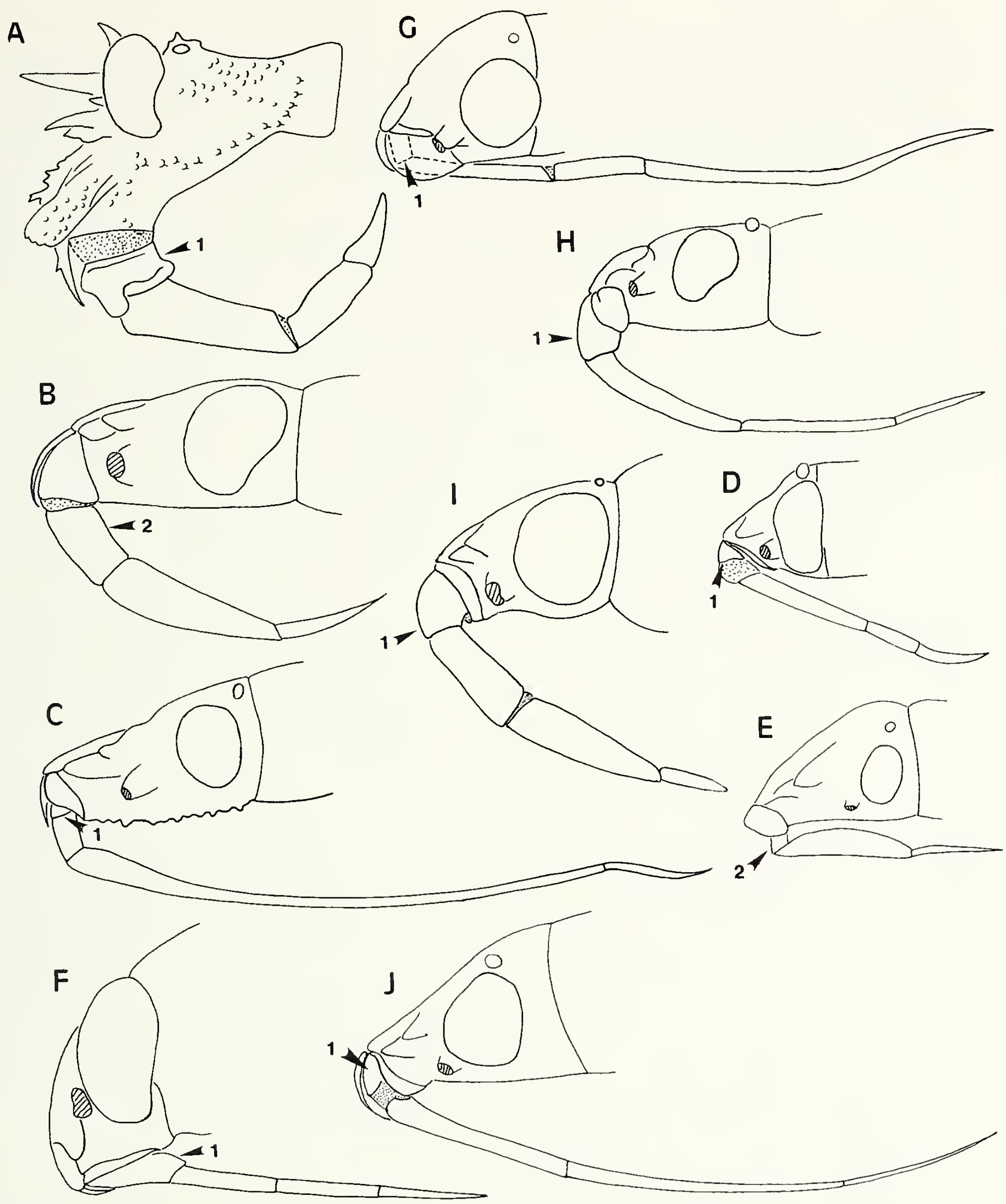

Fig. 5. Lateral view of heads of selected taxa of Cimicomorpha, illustrating conditions described for characters 9 and 10. **A,** Reduviidae, Centrocneminae (*Neocentrocnemis signoreti*; redrawn from Miller [1956a]); **B,** Pachynomidae (*Camarochilus* sp.); **C,** Velocipedidae (*Scotomedes alienus*; redrawn from Kerzhner [1981]); **D,** Microphysidae (*Chinaola quericola*); **E,** Joppeicidae (*Joppeicus paradoxus*); **F,** Miridae, Pilophorini (*Druthmarus philippinensis*; redrawn from Schuh [1984]); **G,** Medocostidae (*Medocostes lestoni*; redrawn from Štys [1967a]); **H,** Nabidae, Nabinae (*Nabis ferus*; redrawn from Kerzhner, [1981]); **I,** Nabidae, Prostemmatinae (*Pagasa guttula*; redrawn from Kerzhner [1981]); **J,** Lyctocoridae (*Lyctocoris campestris*).

and all cimicoid families except the Polyctenidae, in which segment 1 is developed similarly to segments 2–4. The reader should refer to Figure 5 for illustrations of selected taxa.

9. Labium type 0 (straight, appressed to ventral body surface, with segments 3 and 4 relatively long) occurs in the strictly phytophagous family groups, the predominantly phytophagous Miridae (Fig. 5F), and the Vianaidinae and Medocostidae (Fig. 5G) of unknown feeding habits. However, the labium in *Baclozygum,* in contrast to other

Thaumastocorinae, is extremely short, hardly exceeding the base of the head. Labium type 2 (Pachynomidae, Reduviidae; Fig. 5A, B, respectively), in addition to shortness, stoutness, and strong curvature, is characterized by its inflexibility (Cobben, 1978); the articulation between segments 2 and 3 is secondarily flexible in the Reduviidae, Triatominae (Lent and Wygodzinsky, 1979). Under character state 1 we have lumped all of the other admittedly rather diverse types of flexible, curved, or at least angularly bent labia, the subdivision of which (regardless of whether based on relative lengths of segments 2–4, type of curvature, or combination of both features) would have yielded only autapomorphies or imprecisely defined states.

Rieger (1976) and Kerzhner (1981) commented on the great similarity of shape and length of the labial segments in some Dipsocoromorpha (*Ceratocombus*), most Gerromorpha, Ochteridae, Aphelocheiridae, Saldidae, and cimicomorphans in the families Velocipedidae and some Lasiochilidae (*Lasiocolpus*; classified in the Anthocoridae *s. l.* by Kerzhner, 1981). The labium in these groups is characterized by short segments 1 and 2, a strikingly elongate segment 3, and a short segment 4 (Fig. 5C, J). Furthermore, the labium is essentially straight with a striking angularity between segments 2 and 3. Kerzhner (1981) regarded this type of labium as plesiomorphic within the Heteroptera and associated its function with the behavior of a searching predator; he further commented that the above mentioned groups never have raptorial forelegs. Kerzhner (1981) in his dendrogram regarded the velocipedid type of labium as unique among the Cimicomorpha, but inexplicably did not regard it as part of the ground plan for the clade including the Lasiochilidae. We found that the Joppeicidae, some Lasiochilidae (*Lasiochilus*), and some Anthocoridae *s. s.*, have essentially the same type of labium, but with the differences in the relative lengths of segments 3 and 4 not so great as in the Velocipedidae. The same is true for Lyctocoridae and Cimicidae, except that in them labial segment 2 is rather long. Segments 2, 3, and 4 are often subequal in length in the Microphysidae, Nabinae, Prostemmatinae (Fig. 5D, H, I); in the Microphysidae segment 2 is usually longest and segment 4 shortest (Fig. 5D; segment 4 is longest in *Ciorulla* [Péricart, 1974]). The Plokiophilidae are characterized by segment 4 being longer than the others (Carayon, 1974: figs. 11, 12), an attribute shared only with the Medocostidae. The Polyctenidae (coded 1 as well) are unusual in having an almost flaplike labium with all segments subequal in length (Ferris and Usinger, 1939: fig. 4).

10. The labial insertion in the Cimicomorpha can be divided into two more or less distinct types. In those groups in which most members are phytophagous the labium is inserted on the ventral surface of the head and at least the apex of the anteclypeus (tylus) is more or less vertical (Fig. 5F), except in most Thaumastocoridae (e.g., Slater and Schuh, 1990: fig. 1). The predatory groups have the labium inserted anteriorly on the head in a prognathous fashion, with the topographically upper surface of segments 1 or 2 often directed anteriorly and exceeding the apex of the anteclypeus; the anteclypeus is nearly horizontal (Fig. 5A–E, G–J). The only exception is the Polyctenidae with the base of the labium shifted far onto the ventral surface of the head (Ferris and Usinger, 1939: figs. 1, 4).

Thorax

11. The prosternal stridulatory sulcus is absent in several genera of Reduviidae (Miller, 1956b), but nonetheless appears to be part of the ground plan of the group.

Although we have coded the Thaumastocoridae as having the prosternal stridulatory groove, it is not present in all taxa and there is no evidence that it is in fact stridulatory. In *Discocoris* the groove extends onto the mesosternum (labium correspondingly long or longer) (pers. obs.). A similar situation may obtain in *Wechina* (Thaumastocorinae) were the labium exceeds the prosternum. The prosternum is provided with a medial longitudinal ridge in *Baclozygum* (Thaumastocorinae) with the labium being extremely short and not extending onto the prosternum (Drake and Slater, 1957).

12. In the Polyctenidae, nearly the entire metathoracic pleuron is modified into an evaporatory area but there is no distinct groove. A linear transverse slit parallels the anterior margin of the metapleuron but with no apparent connection to any internal structure (pers. obs.). Carayon (1971) confirmed the absence of the metathoracic scent gland groove in the Plokiophilidae, Microphysidae, and its strong reduction in the Pachynomidae and Reduviidae. Carayon and Villiers (1968) noted that in the Reduviidae a conspicuous groove on the metathoracic pleuron is actually associated with Brindley's gland rather than the true metathoracic scent gland.

13. The occurrence of paired metathoracic scent gland reservoirs (always combined with the presence of 2 widely separated ostioles [Carayon, 1971]) in Cimicomorpha is known in the Tingidae *s. s.*, Vianaidinae, Joppeicidae, Pachynomidae, and Reduviidae (Drake and Davis, 1960; Davis and Usinger, 1970; Carayon, 1971) and also in some Miridae, according to Staddon (1979). This type also occurs uniquely in the genus *Leptocimex* (Cacodminae) among the Cimicidae (Carayon, 1966). Davis and Usinger (1970) thought that the paired reservoirs of the metathoracic scent glands in the Joppeicidae possibly do not form a part of the usual metathoracic scent gland system, but belong to the so-called "ventral glands" which open at the thoracicoabdominal junction and are known to occur among the Cimicomorpha in the Reduviidae only; however, Carayon (1971) refuted this conjecture. We had to code the ground plan condition in the Leptopodomorpha as unknown since the situation in this infraorder (Cobben, 1970) is diverse, e.g., number of reservoirs/number of ostioles: Saldidae 1/1; Aepophilidae 2/2; Omaniidae 4/1; Leptopodidae: Leptopodini 2/2, Leotichiini 1/2 (unknown in Leptosaldinae).

14. Information concerning the presence of Brindley's gland is taken from Carayon (1950a), Drake and Davis (1960), and Carayon and Villiers (1968).

Abdominal Trichbothria

15. Ventral abdominal trichobothria in the Pachynomidae were first noticed by Štys in 1964, and subsequently mentioned in passing in the literature, with the first detailed documentation by Carayon and Villiers (1968). Ventral abdominal trichobothria in the Velocipedidae were discovered by Sweet (ms.) and their occurrence confirmed by us. Their position resembles that shown by Carayon and Villiers (1968: fig. 7) for the Pachynomidae, only they are situated closer to the abdominal midline, stiffer and much shorter. Carayon (1972b) suggested that some long, marginal to submarginal setae on the distal abdominal segments in the Anthocoridae *s. l.* and some other families, are of a trichobothrial nature; however, their true nature is yet to be demonstrated and they are surely not homologous with the medioventral trichobothria.

Legs

16. In nearly all groups for which the fossula spongiosa (for illustrations, see e.g., Lent and Wygodzinsky, 1979: fig. 17b, c; Carayon, 1972a: fig. 35) is indicated as present, there may be considerable variation on which legs it occurs, and not all species of a given group may possess the structure, or its occurrence may be limited to males. This structure is present in all families placed conventionally in the Cimicoidea, Nabidae *s. l.*, and Reduvioidea, including the Plokiophilidae and Polyctenidae (confirmed by our observation of specimens of *Lipokophila* sp. and *Eoctenes spasmae*, respectively). Detailed distribution for the fossula spongiosa in Kerzhner's (1981) broadly conceived Nabidae is as follows: Velocipedidae—absent; Medocostidae—vestigial on foretibia in males (not noticed in females by Štys (1967a); Nabinae—Nabini: fore- and middle tibiae in most genera (rudimentary in *Vernonia* and *Kerzhneria*), absent in *Metatropiphorus*; Carthasini: fore-, middle, and hind tibiae in *Carthasis*, fore- and middle tibiae in *Praecarthasis*; Gorpini: rudimentary on foretibia; Arachnocorini: absent in *Arachnocoris* (rudimentary on foretibiae in *Pararachnocoris*? [Kerzhner, pers. comm.]); Prostemmatinae—fore- and middle tibiae.

The tibial appendix in the Thaumastocorinae appears to be of a fundamentally different structure from the fossula spongiosa in other Cimicomorpha. It arises from a different part of the apex of the tibia as illustrated by Drake and Slater (1957: fig. 8). As emphasized by Kerzhner (1981) and confirmed by us, it is covered by unmodified hairs over its entire surface, rather than by modified microtrichia on the ventral surface only.

17. We have coded the number of tarsal segments according to what appears to be the ground plan condition for a given family. Within the Miridae, 2-segmented tarsi occur in all Isometopinae, Psallopinae, and some Cylapinae and Bryocorinae; because the Isometopinae appear to be the sister group of all other Miridae, we have treated the ground plan condition as 2-segmented. In the Plokiophilidae *Lipokophila* has 3-segmented tarsi (as found in most Cimicoidea), whereas in all other described genera the tarsi are 2 segmented. In the Nabinae Carthasini the *Carthasis* tarsal formula is 1-1-1, *Praecarthasis* 2-2-3 (Kerzhner, 1981, 1986). The tarsal formula is usually 3-3-3 in the Reduviidae, but in the Phymatinae, Phimophorinae, and Stenopodainae *partim*, it is 2-3-3 or 2-2-2, in the Reduviinae, 1-3-3, 2-3-3, or 3-3-3 (Putchkov, 1987), and in the Apiomerinae, Diaspidinae, and Ectinoderinae, the foretarsus may be 1- or 2-segmented or absent.

Ferris and Usinger (1939) correctly observed that the adult tarsal formula in the Polyctenidae is 3-4-4 and we have observed that in larval forms the tarsal formula is 2-3-3. Both of these conditions are unique within the Heteroptera. The additional segments are always the result of the separation of the basal portion of the distitarsus, understood here as a tarsomere without intrinsic musculature, articulating with the basal tarsal segment (basitarsus), and bearing the pretarsus. The novel segment in both larval and adult Polyctenidae is recognizable not only by its proximal position but also by the absence of pilosity. In other adult terrestrial Heteroptera the distitarsus is 1- or 2-segmented while in adult Polyctenidae it is 3-segmented on the middle and hind legs. The situation in adult Heteroptera when all tarsi are 1 segmented (some Enicocephalidae, Nepomorpha, and Nabidae) or the foretarsi only are 1 segmented (most Enicocephalomorpha, some Reduviidae and Nepomorpha), has not

been sufficiently well analyzed. These conditions may result from the complete suppression of the basitarsus or from its fusion with a nonsubdivided distitarsus.

18. Of the modern morphologists who discussed rotatory and cardinate metacoxae (occurring in so-called trochalopodous and pagiopodous Heteroptera, respectively), both Drake and Davis (1960) and Cobben (1978) agreed that this historical distinction is somewhat artificial and that intermediate types exist. Cobben (1978) emphasized that the really important distinction is the presence or absence of a trochantin. Nevertheless, the external shape and mobility of the metacoxa in the Cimicomorpha are so diverse that we attempted to include the forms originally recognized by Schiødte (1870), but also included intermediate types. In the case of the Nabinae, which possess cardinate and intermediate types, and the Reduviidae which possess rotatory and intermediate types, we coded each group for the modal condition. Even with this attempt at more precise characterization, the coxae appear to contain little or no information of phylogenetic value and we therefore did not include them in our final analysis.

Wings

19. We have treated the costal fracture as part of the ground plan for the Heteroptera, owing to its occurrence in some members of all infraorders, except the Gerromorpha and Pentatomomorpha. The Saldidae and some other leptopodomorphans possess a well developed costal fracture which arcuately joins the medial furrow (e.g., Polhemus, 1985: fig. 29e, f, h), delimiting an elongate triangular cuneus; we have therefore coded the Leptopodomorpha as having a cuneus, although it is never referred to as such in the literature.

Within the Cimicomorpha, the suggestion that the presence of a long costal fracture (=cuneal incisure, cuneal fracture) demarcating a cuneus can be used to form a group uniting the Microphysidae, Miridae, and Cimicoidea *s. s.* appears to be contradicted by our analysis, by virtue of overlooking the presence of this structure in other cimicomorphans (Velocipedidae, Prostemmatinae, Pachynomidae). The occurrence of the costal fracture in the Pachynomidae (present in *Pachynomus, Punctius*) and Prostemmatinae (present but usually very short in some *Pagasa* and *Prostemma*) is not constant. Because some members of both groups possess the costal fracture, we have coded them as if all members possessed it. The costal fracture in *Punctius* and the Prostemmatinae just interrupts the costal margin, or is rarely longer (Kerzhner, 1981; pers. obs.); it is rather short in *Pachynomus* as well, and there is no distinct cuneus (Carayon and Villiers, 1968; pers. obs.).

20. Most known specimens of Vianaidinae are strongly coleopteroid, and therefore the attributes of venation in the forewing are almost totally obscured. As mentioned above, macropterous specimens have a carinate medial vein running the entire length of the corium similar to the situation found in *Joppeicus paradoxus.* This condition also appears to exist in most, if not all Tingidae *s. s.,* even though the forewings are highly modified and the condition in the Cantacaderinae is somewhat complex. Because of this observation, and the apparent close relationship of the Tingidae *s. s.* and Vianaidinae on the basis of other attributes, we have coded the former group as possessing the carinate medial vein.

21–22. Venation of the forewing membrane has traditionally been used to diagnose higher taxa and establish phylogenetic relationships in the Cimicomorpha. However,

recognition of clearly defined character states has proved difficult. Therefore, we offer some explanatory remarks and survey briefly the situation in individual families.

Carayon (1977b) recognized two basic types of veins in the membrane: live veins which retain living cells throughout the adult life of the insect, contain neurons and are provided with sensilla; and dead veins, which contain no living cells and are devoid of sensilla. Kerzhner (1981, including fig. 98) studied this character complex comparatively and employed it in his phylogenetic analysis of the Cimicomorpha, using as a criterion for live veins the presence of macrotrichia and/or campaniform sensilla. According to him the ancestral situation obtains in the Leptopodomorpha (e.g., Saldidae) with 4, elongate, simple cells formed by live veins. In three families of Cimicomorpha cells formed by live veins are preserved: Velocipedidae with 3 or 4 short live cells (cell 1, beginning at the costal margin, open, if present; closed cells 2, 3, and 4 always present); Miridae usually with 2 short live cells (cell 1, and fused 2–4); and Microphysidae with 1 short live cell (fused cells 2–4). Kerzhner assumed that all other membrane venation in the aforementioned families is dead, and that in the Medocostidae, Nabinae, Prostemmatinae, and cimicoid families the original live cells have been compressed into a vein forming the boundary between the corium and membrane and diverging slightly onto the membrane distad of the cuneus and terminating there as a "stub" (*processus corial*; Carayon, 1974, 1977b), homologous to a similar structure found in the distal corner of cell 2 in the Velocipedidae and of fused cells 2–4 in the Microphysidae. The Pachynomidae, Reduviidae, and Joppeicidae, Tingidae, and Thaumastocoridae should have no live venation on the membrane or at the corium-membrane boundary under Kerzhner's theory.

As mentioned elsewhere in this paper, when we tried to code Kerzhner's theory of membrane venation into clear-cut character states, we found little congruence with other characters. We concluded that a more traditional interpretation of membrane venation showed greater consistency with other characters. Under our hypothesis the membrane cells in the Medocostidae, Nabinae, Prostemmatinae, Pachynomidae, and Reduviidae could be viewed equally well as derived from the original elongate cells. The venation of many Phymatinae, with short basal cells and many emanating veins, is strongly reminiscent of the condition found in the Velocipedidae. The simple membrane venation occurring in some reduviid taxa is best explained by the subsequent opening of the cells as, e.g., in the Elasmodeminae (Putchkov, 1987; pers. obs.).

We found the "stub" (processus corial), first employed as a systematic character by Kerzhner (1981), to be particularly useful. This rounded to truncate projection (or termination) of a vein is situated distad of the cuneus and never reaches the costal margin of the membrane. In many Lasiochilidae and Anthocoridae the membrane venation is reduced, and the stub or its remnant appears as a semisclerotized bulgelike structure isolated on the membrane (Fig. 7F). Although the stub is barely visible on the upper wing surface in the Prostemmatinae, it is sharply delimited on the lower forewing surface, appearing as an elongate, slightly raised, platelike structure.

The venational details of individual families can be characterized as follows:

Velocipedidae: Cells 2, 3, and 4 present but abbreviated and situated at base of membrane. Cell 1 open (absent) or closed by a feeble rudimentary vein; numerous veins radiating posteriorly from the cells; stub present on apex of cell 2, easily visible on lower wing surface (Fig. 6D; Kerzhner, 1981: fig. 24).

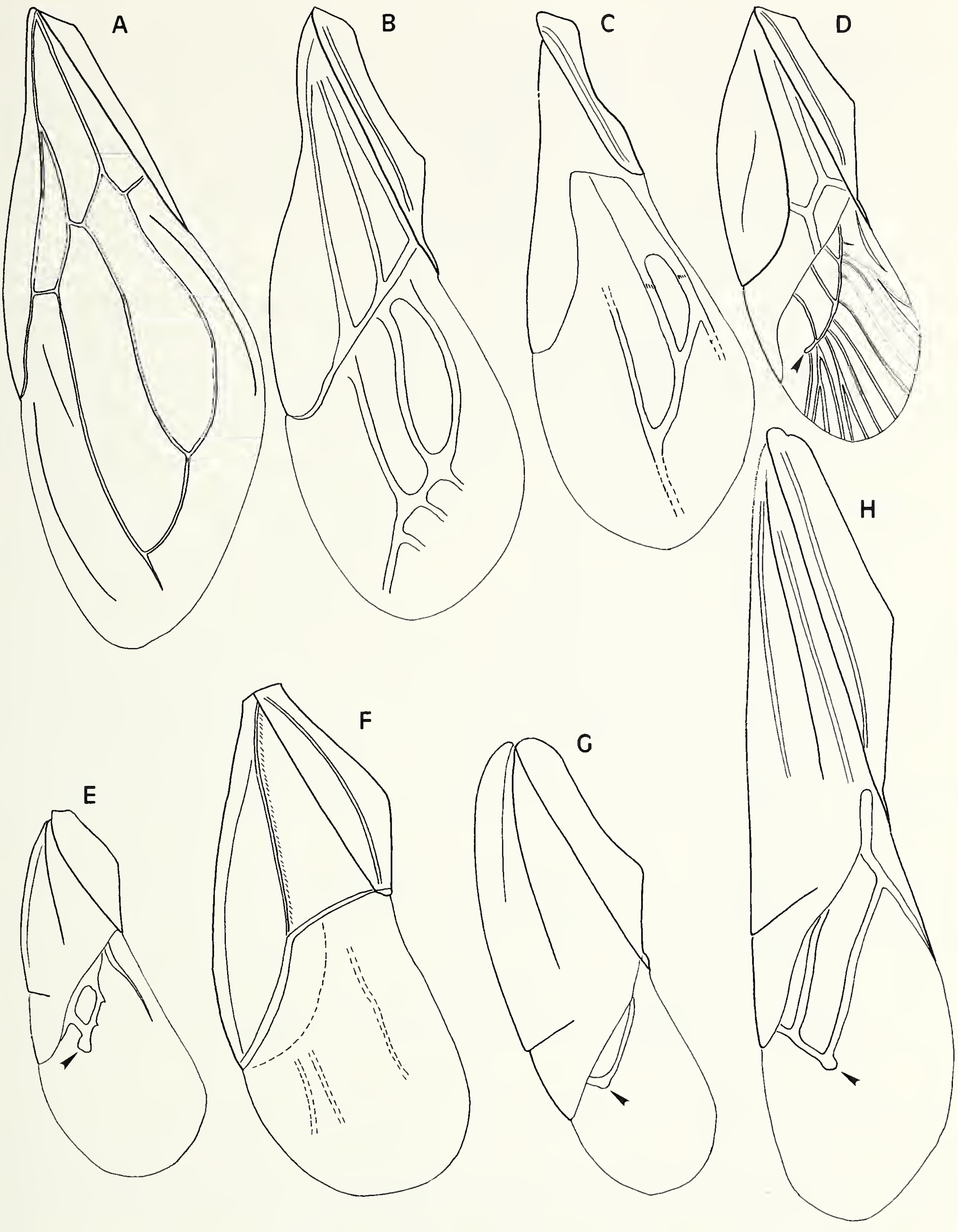

Fig. 6. Forewings of Cimicomorpha, demonstrating essential attributes of corium and clavus and details of membrane described for characters 21 and 22. **A,** Reduviidae, Triatominae (*Triatoma guazu*; redrawn from Lent and Wygodzinsky [1979]; **B,** Pachynomidae, Pachynominae (*Camarochilus* sp.); **C,** Pachynomidae, Aphelonotinae (*Aphelonotus* sp.); **D,** Velocipedidae (*Scotomedes* sp.); **E,** Microphysidae (*Myrmedobia exilis*); **F,** Joppeicidae (*Joppeicus paradoxus*; modified from Davis and Usinger [1970]; **G,** Miridae, Isometopinae (*Corticoris signatus*); **H,** Miridae, Cylapinae (*Cylapus* sp.). Position of stub indicated by arrow.

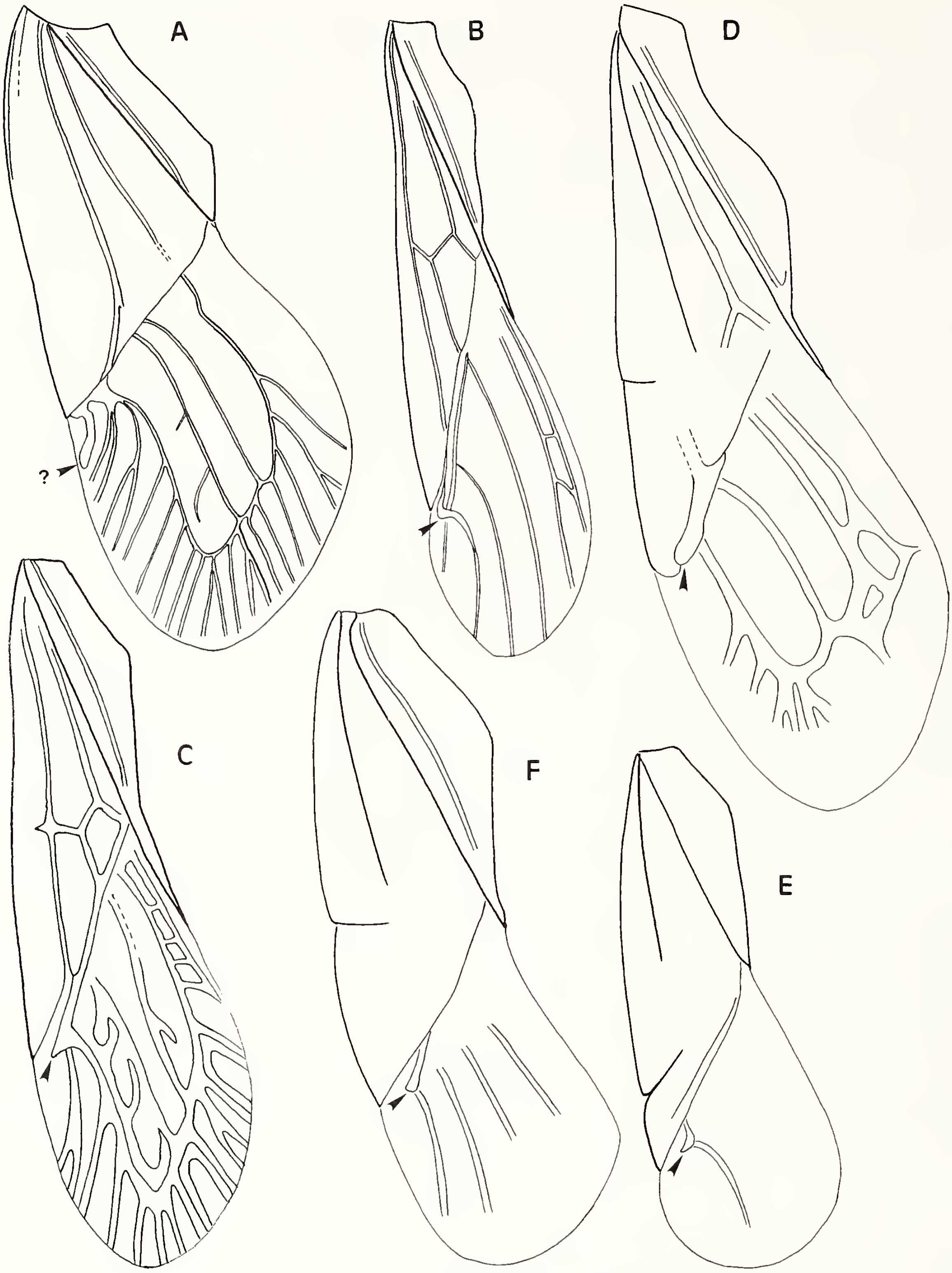

Fig. 7. Forewings of Cimicomorpha, demonstrating essential attributes of corium and clavus and details of membrane described for characters 21 and 22. **A,** Medocostidae (*Medocostes lestoni*; redrawn from Štys [1967a]; **B,** Nabidae, Nabinae (*Metapterus alvarengai*); **C,** Nabidae, Nabinae (*Nabis americoferus*); **D,** Nabidae, Prostemmatinae (*Pagasa luteiceps*); **E,** Plokiophilidae (*Lipokophila* sp.); **F,** Lyctocoridae (*Lyctocoris campestris*). Position of stub indicated by arrow.

Miridae: Two abbreviated cells (Fig. 6H) (under Kerzhner's interpretation, 1 adjacent to cuneus, fused 2+3+4 medial) sometimes merging into a single cell, e.g., some Isometopinae (Fig. 6G) and Bryocorinae. Usually no longitudinal veins except a single one near the morphologically posterior margin of the membrane, rarely a

few simple veins emanating from the posterior margin of the large cell in some large Mirini and a few Odoniellini (Bryocorinae) (Carayon, 1977b; fig. 1); stub present at distal angle of cell(s). Carayon (1974, 1977a) considered the membrane veins in part to represent the stub (processus corial) and indeed our observations (Fig. 6G, H) indicate that his observation may be correct.

Microphysidae: One short, more or less quadrate, cell (fused cells 2–4 ?) formed of strongly sclerotized veins, situated medially at the base of the membrane, remote from cuneus, with 4 or 5 longitudinal veins emanating posteriorly and 1 free simple posterior vein; stub present at apex of cell (Fig. 6E; Péricart, 1972: fig. 9a).

Medocostidae, Nabinae, Prostemmatinae: Two or 3 long cells (not associated with apicocorial area), with many emanating veins (Fig. 7A–D); cells open and venation simplified in various Nabinae and Prostemmatinae (Phorticini; Štys, pers. obs.); stub present (absent in at least some Phorticini), often elongate, associated with corium–membrane boundary (Nabidae—Kerzhner, 1981: fig. 26) or slightly removed (Medocostidae—Štys, 1967a: fig. 21; Fig. 7A).

Pachynomidae: Two, long, "reduvioid" cells with many emanating veins (*Pachynomus*) or emanating veins faint and few (*Camarochilus*) or reduced to 1 (*Punctius, Aphelonotus*); no stub (Fig. 6B, C).

Reduviidae: Two or 3 long closed cells with or without 1 emanating vein and with or without 1 free posterior vein (Fig. 6A), rarely with 4 free veins (Elasmodeminae) or with 2 short basal cells (sometimes more numerous and variable in number) with many emanating veins and 2 posterior free branching veins (Phymatinae); no stub (Fig. 6A). Although Kerzhner (1981) treated all reduviid venation as dead, Davis (1961) clearly showed tracheation of membrane cells in the group.

Lasiochilidae, Lyctocoridae, Anthocoridae: Four or 5 simple free veins; stub present, associated with corium (cuneus)-membrane boundary, sometimes detached (Fig. 7F).

Plokiophilidae: Membrane sometimes apparently with 1 or 2 elongate cells (Carayon, 1974: figs. 5, 7), or closed cells absent and a single vein projecting distally from stub (Fig. 7E); stub present, projecting from corium-membrane boundary (Carayon, 1974: fig. 31; Fig. 7E).

Joppeicidae: Large transverse cell formed by a fold (foldlike vein ?), with 2 emanating simple veins and 1 free posterior vein; no stub (Fig. 6F); Drake and Davis, 1970: fig. 6).

Tingidae *s. s.*: Major longitudinal veins continuing onto membrane area (not differentiated from corium); no special membrane venation; no stub (Drake and Davis, 1960: fig. 13).

Vianaidinae: No membrane venation, no stub, including macropterous forms (pers. obs.).

Thaumastocoridae: No membrane venation; no stub (Drake and Slater, 1957; pers. obs.).

23. The distal free sector of R+M (emanating from the hind wing cell) is usually simple in the Cimicomorpha. However, Davis (1961) and Štys (1962) found that it branches into free distal sectors of R and M in the Nabinae and Microphysidae. Štys (1967a: fig. 25) found that R+M has several short lateral branches in the Medocostidae, but the morphological identity of the distal branching veins seems in doubt. Carayon (1970), on the basis of studying the tracheation of the Nabinae suggested

that the posterior sector of the branching R+M is actually only a secondary branch of the media, its major part remaining captured by R. On the other hand, Leston (1962) concluded that the distal sector of veins R, M, and Cu is not tracheated at all. The illustration of the hind wing of *Pachynomus picipes* by Carayon and Villiers (1968) suggests inconclusively that branching R+M may also occur in some Pachynomidae, but because it does not occur in other genera, we coded it as absent in the family.

24. The media (as interpreted by Davis, 1961) in the hind wing runs within the closed cell and meets as a long vein or a stumplike hamus either Cu or the point where the free distal sector of Cu diverges from the cell (in these two cases the "cross vein" closing the cell and meeting R is actually formed by M), or joins the above "cross vein" (e.g., Davis, 1961: fig. 16); in the latter case the "cross vein" is formed in part by a true cross vein m-cu and in part M. The presence of a true m-cu cross vein is characteristic of most families of Cimicomorpha as shown in the matrix. However, its presence in Plokiophilidae (documented in *Lipokophila* sp. only), Anthocoridae (Carayon, 1972a), Pachynomidae (Carayon and Villiers, 1968), and Reduviidae is a ground plan character only and the situation in all of these families is diverse. Davis (1961: fig. 29) illustrated the hind wing of *Scotomedes ater* (Velocipedidae) as lacking m-cu, but it is definitely present in a species of Velocipedidae from New Guinea. In several families of Cimicomorpha the true m-cu cross vein seems to be consistently absent: Microphysidae, Miridae, Joppeicidae, Thaumastocoridae, and Tingidae. We include here also the groups where any remnant of M within the cell is missing and M is represented only by a transverse vein closing the cell. Data for the matrix were extracted from Davis (1961), Štys (1967a), Carayon and Villiers (1968), Kerzhner (1981), and Carayon (1972a); the condition in the Velocipedidae and Plokiophilidae was reexamined.

Abdomen

25. The presence of dorsal laterotergites is undoubtedly part of the ground plan of the Cimicomorpha. However, in some taxa these structures are found associated with only certain abdominal segments, e.g., in the Lasiochilidae as distinct entities on abdominal segments 1 and 2 only (Carayon, 1972a). In such cases we have coded dorsal laterotergites as present for the taxon. The unusual structure of the abdomen in the Joppeicidae (Davis and Usinger, 1970: figs. 8, 12) has caused confusion concerning whether the distinct laterotergites are dorsal or ventral in origin; we have followed Sweet (1981) in interpreting them as dorsal. The abdominal dorsum in the Microphysidae is desclerotized in the males and sclerotized in the females, but distinct laterotergites are not present. The presence of dorsal laterotergites in the Plokiophilidae is based on observation of *Lipokophila* sp. According to Carayon (1972a) all of the Lasiochilidae, Lyctocoridae, and Anthocoridae have dorsal laterotergites at least on some segments, with the exception of *Astemmocoris,* a genus of questionable placement.

26. As with the dorsal laterotergites, if the ventral laterotergites are present at least in some taxa, or some segments only, or in males only, they were coded as present. The ventral laterotergites in the Velocipedidae are present only in the males (Sweet, ms; pers. obs.), but are not evident in the females and apparently fused with the sternum. We consider the ventral spiracle bearing plate in the Joppeicidae to represent

the fusion of the sternum and the ventral laterotergites (Sweet, 1981). Although the ventral laterotergites are coded as being absent in the Prostemmatinae, the original boundary of the structure is demarcated by a ridge on the venter in the Phorticini. We have coded these structures as present in the Nabinae, although they are absent in some genera. The Polyctenidae are unusual among the Cimicoidea in the possession of ventral laterotergites.

27. The presence or absence of the first abdominal spiracles, as coded in the data matrix, seems unproblematic, except for the taxa discussed below. The occurrence of the first abdominal spiracle in the Thaumastocorinae was noted by Drake and Slater (1957). Its occurrence was confirmed by us in the sclerotized lateral part of the first tergum of *Discocoris* (Xylastodorinae); it was observed in the membrane between the metanotum and the first abdominal tergum of *Thaumastocoris australicus, T. hackeri* (Thaumastocorinae) and *Xylastodoris luteolus* (Xylastodorinae) by Sweet (ms). It is not apparent that any of these observations include the documentation of tracheal connections. The absence of the first abdominal spiracle in the Joppeicidae, as indicated in the matrix, was noted by Davis and Usinger (1970). The absence of the first abdominal spiracle in the Microphysidae and Velocipedidae was confirmed by our own examination of *Myrmedobia exilis* (see also Štys, 1962) and *Scotomedes* sp., respectively.

28. Our observations on spiracle positions on the abdomen confirm those of Sweet (ms). We have coded the Joppeicidae as in other Miriformes and Cimiciformes where the spiracles are situated on a sclerite formed by the fusion of the sternum and the ventral laterotergite. Alternatively, in the Reduvioidea, the spiracles are situated on the true sternum, mesad of the line delimiting the ventral laterotergites.

29. Fossettes parastigmatiques (parastigmal pits) were first discovered by Carayon (1948: figs. 1, 2; 1950b: figs. 1, 2). These small structures are situated on the ventral laterotergites and contain a cluster of secretory hairs; their function is unknown. They occur in Nabinae (Nabini and some Carthasini [*Praecarthasis* Kerzhner, 1981, 1986], on segments 3–7 with the most restricted occurrence on segment 7 only, but are absent in *Carthasis,* Arachnocorini, and Gorpini) (Kerzhner, 1981; Carayon and Villiers, 1968). In the Prostemmatinae, Prostemmatini they occur as a single pair on segment 3 and are absent in the Phorticini (Kerzhner, 1981). Similar appearing structures are found on the second abdominal segment in the Pachynomidae, Aphelonotinae, and as less well formed structures in the Pachynominae, whereas they are completely absent in *Punctius* (Carayon and Villiers, 1968). Kerzhner (1981) presumed that the fossettes parastigmatiques in Nabidae and Pachynomidae are homologous and that they are secondarily absent in the Reduviidae; both conclusions appear to be incorrect in light of our analysis.

30. The apophysis is a small anteriorly directed, median, internal projection of the anterior margin of abdominal sternum 7 in the female. Its distribution is based on the works of Štys (1967a: fig. 43), Carayon and Villiers (1968), Carayon (1972a), Ford (ms), and Kerzhner (1981). It is apparently secondarily absent is the Arachnocorini (Nabinae).

31–34. Cobben (1978:141, table 2) summarized the distribution of the dorsal abdominal scent glands in larval Heteroptera. We checked the distribution in all families where Cobben's summary was ambiguous or lacked information entirely (Thaumastocoridae, Velocipedidae [first observation of actual larval gland openings],

Microphysidae, and Polyctenidae). In the Lasiochilidae (our observations), Medocostidae (Štys, 1967a), and Pachynomidae (Cobben, 1978), the recorded occurrence is based on the presence of scars in the adult abdomen because larvae are unknown or unstudied. The orifices of glands 3/4, 4/5, and 5/6 in larvae are always associated with the actual glands. Orifices between segments 6 and 7 have functional inner glandular parts only in the Joppeicidae; external nonfunctional scars of orifices on 6/7 remain in several additional families. The determination of whether scars actually exist is sometimes a subjective judgment, and therefore no great value can be placed on this character. Scars and glands are usually located on the anterior margin of the more posterior segment. Most observers have not found larval abdominal scent glands in the larvae of the Polyctenidae. Ferris and Usinger (1945) noted that dorsal scent glands were present on the posterior margins of abdominal segments 4, 5, and 6 (clearly a *lapsus calami* for "anterior margins") in some larval Brazilian specimens, and that the glands resembled those of the Cimicidae.

35. Ekblom's organ, a structure first noticed by Ekblom (1926: figs. 56, 57) and later named for its founder by Kerzhner (1981: fig. 60b), occurs in males of all Prostemmatinae and most Nabinae (Kerzhner, 1981). It consists of two diagonal grooves surrounded by specialized setae situated behind the posterior foramen of the pygophore (Carayon, 1970: fig. 20) and a group of specialized setae at the posteroapical margin of the hind femur. Males possessing the organ rub the tibiae across the pygophoral portion of the organ and distribute attractant pheromones from intrarectal glands (Carayon, 1970); previously the organ was thought to be part of a stridulatory apparatus (Ekblom, 1926), but Leston (1957) considered such a function unlikely.

36. The data from Kerzhner (1981) regarding reduction of abdominal segment 8 in males are accepted here and have been reconfirmed by us for several families. We have coded this character as occurring in the primitive condition in the Nabinae, because it is found in that condition in *Metatropiphorus,* the genus which Kerzhner believed to be the most primitive within the Nabinae (Nabini).

Genitalia and Insemination

37. Male terminalia (essentially the pygophore and parameres) are asymmetrical in several families; we recognize three types, each of them appearing to have evolved independently. In the thaumastocorid type, (state 2), described by Drake and Slater (1957: figs. 6, 8, 11), the pygophore is strongly asymmetrical and turned laterad, the asymmetry strongly affecting one or more abdominal segments anterior to 9, one or both parameres are lost, and the asymmetry is either sinistral or dextral. In the mirid type (state 1) the parameres and pygophore are asymmetrical, the asymmetry is always sinistral but not affecting the abdominal segments anterior to the pygophore, both parameres are retained and never lanceolate or horizontal. In the cimicoid type (state 3), except in the Plokiophilidae, the sinistral asymmetry affects the parameres and pygophore, but abdominal segment 8 is at most slightly asymmetrical, the left paramere is dominant, more or less lanceolate, and its blade is oriented horizontally and directed more or less perpendicular to the longitudinal axis of the pygophore.

In some families where parameres are usually symmetrical, there are isolated cases of asymmetry, e.g., in most Peiratinae (Reduviidae) and some Nabinae and Pros-

temmatinae (Kerzhner, 1981). In all of these cases we consider the ground plan condition to be symmetrical. In some groups one of the parameres, usually the right, has been lost completely. These include all of the Cimicidae and Polyctenidae (see e.g., Ferris and Usinger, 1939; Usinger, 1966), and some Lasiochilidae and Anthocoridae (Carayon, 1972a). In the Thaumastocorinae, only one paramere is present, being either the right or the left (genus specific or species specific attribute), while in the Xylastodorinae the same species may be dextrally or sinistrally asymmetrical, with *Discocoris* retaining a single paramere, and *Xylastodoris* uniquely having lost both parameres (see Drake and Slater, 1957). We have regarded the parameres in the Plokiophilidae as symmetrical, and indeed this seems to be the case for most genera. Nonetheless, Štys (1967b) and Eberhard et al. (in prep.) have shown that in the genus *Lipokophila* the parameres are of a slightly different size and shape even though the pygophore appears to be symmetrical; however, Carayon's (1974) illustrations of *Lipokophila* would suggest that the parameres are symmetrical.

38. Carayon (1972a, etc.) and Ford (ms.) have discussed the structure and summarized the distribution of the copulatory paramere in the Cimicoidea. See also notes under character 40 for functional explanation.

39. The orientation of the parameres was used by Kerzhner (1981) as a character and we have employed his data. In the Pachynomidae the basal portion of the parameres points caudad with the distal portion directed cephalomesad. There are other aspects of paramere direction and insertion which could be employed in phylogenetic analysis, but a comparative survey is not available. For example, within the families studied in detail by Kerzhner (1981), the situation is as follows: parameres situated on dorsum or sides of pygophore (and directed cephalad—Velocipedidae and most Nabinae; or cephalomesad—Nabini, *Metatropiphorus*; or dorsomesad—Medocostidae); situated caudad and directed dorsad—Prostemmatinae, Prostemmatini; situated ventrad, owing to ventral position of pygophore, and directed caudad (but morphologically cephalad)—Prostemmatinae, Phorticini.

40. The term acus used by Carayon (e.g., 1972a) refers to the so-called "needle of injection." This is the apical spinelike process of the phallus as found in many Cimicoidea and apparently all Prostemmatinae (e.g., Carayon, 1970a: fig. 26).

For the reader not familiar with the specialized morphology and type of copulation found in the Cimicoidea we offer a brief explanation of the functional relationship between the phallus and left paramere. In the Lasiochilidae, Plokiophilidae, and Lyctocoridae, the phallus itself serves as the intromittent organ; in Lasiochilidae there is no acus and no traumatic insemination, whereas in the Plokiophilidae and Lyctocoridae the acus penetrates the integument of the abdominal wall, and in a similar way penetrates the vaginal wall in the Prostemmatinae. There is a specialized relationship between the phallus and left paramere in the Cimicidae, Polyctenidae, and Anthocoridae, where the left paramere penetrates the abdominal wall or the metacoxal arthrodial membrane of the female and insemination is always traumatic. In these groups, excepting the Anthocorini *sensu* Carayon and Scolopini (*vide* Péricart, 1972), the distal portion of the phallus is reduced to a short membranous tube situated within the parameral groove and serves only for introduction of sperm into the abdominal cavity of the female. In the Anthocorini and Scolopini the phallus is long, not accommodated in the parameral groove and slides into the copulatory tubes of the female (see Carayon, 1966, 1970, 1971, 1977a). In these last two groups the

details of the functional relationship between the phallus and the left paramere needs to be investigated in greater detail (see conflicting reports by Carayon [1972a] and Péricart [1972]).

41. The reduction of the ovipositor in the Cimicomorpha, as for the Heteroptera in general, has occurred many times, as seems obvious from our analysis. In four groups we coded the ovipositor as laciniate, whereas some members of those groups actually have it plate-shaped or greatly reduced. These are: Nabinae, Arachnocorini, *Arachnocoris* (Kerzhner, 1981); Prostemmatinae, excluding Phorticini (Kerzhner, 1981); Lasiochilidae and Anthocoridae, diverse genera (Carayon, 1972a).

Information on the loss of a connection between the first valvula and the first valvifer in those groups with a laciniate ovipositor (character state 1) is taken from Drake and Davis (1960). However, the Microphysidae, coded as having the primitive condition, might not have been investigated for this attribute and should be reexamined.

42. The information on relationships between ventral laterotergite 8 and valvifer I provided in the matrix is based mostly on the information given by Scudder (1959) and Drake and Davis (1960) and supplemented by information on the Pachynomidae (Carayon and Villiers, 1968), Medocostidae (Štys, 1967a), Joppeicidae (Davis and Usinger, 1970), and Prostemmatinae (Kerzhner, 1981). The condition in *Lasiochilus* has not been studied, but the retention of the plesiomorphic condition (ventral laterotergite free) is probable. Kerzhner (1981) observed that valvifer I is fused with laterotergite 8 in some Nabinae (*Arachnocoris*) and Prostemmatinae (Phorticini). The same condition may apply to those Lasiochilidae and Anthocoridae with a reduced ovipositor. In the Tingidae ventral laterotergite 8 is fused with valvifer I, but it is still recognizable as a distinct entity; we coded it as fused.

43. In many cimicomorphans, the spermatheca is transformed into a so-called vermiform gland (in Reduviidae, e.g., Davis, 1966: fig. 39; in Miridae, e.g., as spermathecal gland, Davis, 1955: fig. 7) which has no sperm storage function. *Joppeicus* retains a structure with all the components of a true spermatheca, but it is small and not functioning as a sperm storage structure (Carayon, 1954: figs. 5–7; Carayon in litt. to Kerzhner, 1981; Davis and Usinger, 1970: fig. 17). In the Tingidae *s. s.* a "reduced spermatheca" is present in some Cantacaderinae only (Kerzhner, 1981 [according to Carayon, in litt.]; Péricart, 1983), whereas in other Cantacaderinae and Tinginae it is completely absent. However, Drake and Davis (1960: fig. 15) illustrated a "spermathecal gland" in *Cantacader quadricornis* and considered it to be a reduced vermiform gland. (For organs functionally replacing the spermatheca in the Tingidae see discussion of character 45 below.) We have treated the reduced nonfunctional spermatheca as part of the ground plan of the Tingidae. According to Scudder (1959) and Drake and Davis (1960) the spermatheca (or its homolog) is absent in the Vianaidinae. Kerzhner (1981) quoted Carayon (in litt.) as stating that *Embiophila* (Plokiophilidae) has a typical small spermatheca with a bulb and duct; he considered it as possibly a new structure similar to that occurring in *Plokiophiloides* (Carayon, 1974). We have tentatively accepted Carayon's (1974) opinion concerning the occurrence of a "vestigial spermatheca" in the Plokiophilidae.

44. Information summarized by Carayon (1977a) indicates that spermatolytic bodies are groups of amoebocytes and macrophages located at the bases of the ovarioles. Their function is the destruction and resorption of excess spermatozoa. They are

formed by individual cells in the Prostemmatinae, whereas they are of a syncitial nature in the Cimicoidea.

45. The Reduviidae and Pachynomidae possess paired, tubular pseudospermathecae opening into a median oviduct (Davis, 1966: fig. 36) and serving as permanent sperm storage organs in place of the typical heteropteran spermatheca. In the Pachynomidae these structures are visible only after clearing (Carayon and Villiers, 1968: figs. 26–28), being covered by the muscular tunica of the ovipositor. Analogous paired organs, serving for only temporary sperm storage, are the large, subglobular, paired ectodermal seminal sacs of the Tingidae *s. s.* (Carayon, 1954: figs. 1, 3; Drake and Davis, 1960: fig. 12), opening into a median oviduct (or even the gynatrium) or into the broad proximal ectodermal parts of the lateral oviducts. It is uncertain whether these paired seminal sacs are homologous to the functionally equivalent median unpaired ectodermal dorsal sac (often referred to as the seminal sac [e.g., Carayon, 1954]) of the Miridae and at least some Cantacaderinae (Drake and Davis, 1960: fig. 25). Paired, broadly tubular spermathecal organs associated with the lateral oviducts found by Drake and Davis (1960: fig. 25) in *Cantacader quinquecostatus* jointly with the dorsal sac are of mesodermal origin and are not homologous with psuedospermathecae. Drake and Davis (1960) concluded that a possible homology between pseudospermathecae, seminal sacs, and the dorsal sac is ambiguous, and we regard the true psuedospermathecae of reduviids and pachynomids as structurally and functionally unique.

46–47. The method of fertilization in the Cimicomorpha has been studied in great detail by Carayon with the results presented in numerous papers (1954, 1957, 1966, 1972a, 1977a, etc.). The situation in the Vianaidinae, Thaumastocoridae, Velocipedidae, and Medocostidae is inferred from examination of gross morphology rather than functional studies. Carayon (1962a) pointed out the three different modalities of fertilization which exist in the Cimicomorpha: 1) Reduvioidea—in ectodermal part of the female reproductive tract; 2) most other groups (Tingidae *s. s.,* Vianaidinae, Miridae, Microphysidae, Joppeicidae [*contra* Carayon, 1962a], Lasiochilidae, Nabinae, and Prostemmatinae [the last even in spite of traumatic insemination])—in lateral mesodermal oviducts or in the ovarial pedicels; and 3) cimicoid families less Lasiochilidae—in the vitellarium. Carayon (1972a) stressed the similarity in fertilization between the Prostemmatinae and Lasiochilidae (cf. Carayon, 1957), but did not comment upon what he supposed to be the similarity between the situation in the Joppeicidae and the advanced cimicoid families. Davis and Usinger (1970) examined the mode of fertilization in the Joppeicidae and found that insemination actually takes place according to mode 2, not as in the cimicoid families. Hemocoelic (traumatic) insemination among the Heteroptera is restricted to the Cimicomorpha. In the Cimicoidea it is ordinarily accomplished by penetration of the left paramere and/or phallus through nonspecialized to highly modified regions (i.e., ectospermalege, mesospermalege [also variously referred to as Berlese's organ or Ribaga's organ], copulatory tubes, etc.) of the abdominal wall of the genital or pregenital segments. Only in Polyctenidae are the sperm introduced into the hemocoel via the arthrodial membrane of the right metacoxa. In the Prostemmatinae the vaginal wall is punctured by the phallus. For a summary see Carayon (1977a). See also discussion of character 40. Cobben (1968) alluded to the possibility of accidental traumatic insemination in the Microphysidae and vitellarial insemination in the Velocipedidae (micropyle re-

duced and solid) and Nabinae, Arachnocorini (micropyle absent), but in our view these suggestions require confirmation through additional observation.

Eggs

48. Data for micropyle numbers are from Cobben (1968), who stated that there are no distinct external micropyles in either the Thaumastocorinae or Xylastodorinae and that the aeropylar system seems to be combined with the micropylar system in a different way in each of the two subfamilies. Some Nabinae (Arachnocorini) have lost the micropyles. Cobben (1968) was not sure whether 1 or 2 micropyles occur in the Microphysidae; we have coded 1. The Polyctenidae have pseudoplacental viviparity and do not form a chorion (Hagan, 1931). Davis and Usinger (1970) described the eggs of the Joppeicidae as having 1 micropyle.

Habits

49. For the Vianaidinae, Velocipedidae, and Medocostidae, where no observations on feeding habits are available, we have coded this character as unknown. For the Miridae, even though most species are phytophagous, we have coded the group as predaceous because the most primitive subgroup, the Isometopinae, is predaceous. Some Anthocoridae, especially Oriini, are known to be partly phytophagous.

50. Whereas only the Cimicidae and Polyctenidae are obligatory hematophagous ectoparasites, all Triatominae (Reduviidae) are hematophagous and some *Lyctocoris* species (Lyctocoridae) are at least facultative or possibly obligate blood feeders.

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REVISION OF *KELTONIA* AND THE COTTON FLEAHOPPER GENUS *PSEUDATOMOSCELIS,* WITH THE DESCRIPTION OF A NEW GENUS AND AN ANALYSIS OF THEIR RELATIONSHIPS (HETEROPTERA: MIRIDAE: PHYLINAE)

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Abstract.—The New World genera *Keltonia* Knight, containing 12 species, and *Pseudatomoscelis* Poppius, containing three species and including the cotton fleahopper (*P. seriatus* (Reuter)), are revised, and the new species *Keltonia bifurca, K. mexicana,* and *K. schaffneri* from Mexico, *K. pallida* and *K. robusta* from the United States, *K. steineri* from Grand Bahama Island, *Lineatopsallus slateri* from Texas, and *Pseudatomoscelis insularis* from Puerto Rico and St. Thomas are described. The new genus *Lineatopsallus* is established to accommodate *Psallus biguttulatus* Uhler and the new species *L. slateri. Pseudatomoscelis tuckeri* Poppius is resurrected from synonymy and transferred to *Keltonia*; *Psallus flora* Van Duzee is transferred to *Pseudatomoscelis*; *Psallus conspurcatus* Blatchley and *Keltonia fuscipunctata* Knight are considered junior synonyms of *K. sulphurea,* and *Psallus atomophorus* Reuter, a junior synonym of *P. seriatus*; and revised keys to species of *Keltonia* and *Pseudatomoscelis* are given. A cladistic analysis, using *Lineatopsallus* as the outgroup, indicates that *Keltonia* and *Pseudatomoscelis* are sister genera.

Despite the great amount of economic literature treating the cotton fleahopper, *Pseudatomoscelis seriatus* (Reuter) (Sterling and Dean, 1977; papers cited in Frisbie et al., 1989), little is known of its distribution outside the United States (Sterling et al., 1989), or the relationship of *Pseudatomoscelis* Poppius to other genera within the mirid tribe Phylini (Phylinae). This revision is provided to furnish information on the recognition, distribution, hosts, and relationships of *P. seriatus* and related taxa.

Before 1920, the cotton fleahopper did not attract much attention as a pest of cotton (Reinhard, 1926). Since then, however, *P. seriatus* has ranked among the most important pests of cotton in the United States, possibly behind only the boll weevil (*Anthonomus grandis* Boheman), the bollworm (*Helicoverpa virescens* (F.)), and lygus bugs (*Lygus elisus* Van Duzee, *L. hesperus* Knight, and *L. lineolaris* (Palisot)). Losses to U.S. cotton in 1983 from the *P. seriatus* were estimated at over 46,000 bales, with the greatest crop reductions occurring in Texas, followed in order by Mississippi, Louisiana, New Mexico, Oklahoma, and Arizona (USDA, 1984). Damage results from nymphs and adults feeding on the reproductive structures, causing blasting and shedding of young cotton squares and often abnormal plant growth (Gaylor and Sterling, 1975). Secondary problems can arise when insecticides applied to control the fleahopper eliminate natural enemies, resulting in more severe outbreaks of other pests (Almand et al., 1976). Although most often termed a "key" pest during pre-bloom periods (e.g., Adkisson, 1973; Bottrell, 1973), *P. seriatus* may at other times

reverse its role on cotton to become a "key" predator, especially on the eggs of *Helicoverpa* (as *Heliothis*) species (e.g., McDaniel and Sterling, 1982; Johnson et al., 1986).

Prior to this study, only one species of *Pseudatomoscelis* and only six of *Keltonia* were recognized. Herein, I describe one new species of *Pseudatomoscelis,* six new *Keltonia,* and the new genus *Lineatopsallus* to accommodate *Psallus biguttulatus* Uhler and the new species *L. slateri. Psallus atomophorus* Reuter is considered a junior synonym of *Pseudatomoscelis seriatus,* and *Psallus conspurcatus* Blatchley and *K. fuscipunctata* Knight junior synonyms of *K. sulphurea. Pseudatomoscelis tuckeri* Poppius is resurrected from synonymy, and *Psallus flora* Van Duzee is transferred to *Pseudatomoscelis.* Figures of male genitalia, habitus photos for selected species, habitus illustrations for *K. tuckeri* and *P. seriatus,* scanning electron micrographs of pertinent structures (magnifications given on plates are before reduction to JNYES page format), and identification keys to species of each genus are provided to facilitate recognition. Species of *Keltonia* and *Pseudatomoscelis* are arranged alphabetically in the Systematics Section and are followed by a description of the outgroup and a discussion of relations under the Phylogenetic Analysis.

The following abbreviations are used for institutions cited in this paper: AMNH (American Museum of Natural History, New York, New York, R. T. Schuh, M. D. Schwartz [now at CNC], and G. L. Stonedahl [now at CAB Internatl. Inst. Entomol., London); CAS (California Academy of Sciences, San Francisco, P. Arnaud and N. Penny); CNC (Canadian National Collection, Ottawa, L. A. Kelton and M. D. Schwartz); FSCA (Florida State Collection of Arthropods, Florida Department of Agriculture, Gainesville, F. W. Mead); PDA (Bureau of Plant Industry, Pennsylvania Department of Agriculture, Harrisburg, A. G. Wheeler, Jr.); JTP (J. T. Polhemus Collection, Englewood, Colorado); OSU (Department of Entomology, Oregon State University, Corvallis, J. D. Lattin); PSU (Department of Entomology, Pennsylvania State University, State College, K. C. Kim); PU (Department of Entomology, Purdue University, West Lafayette, Indiana, A. V. Provonsha); TAM (Texas A&M University, College Station, Texas, J. C. Schaffner); KU (Department of Entomology, University of Kansas, Lawrence, P. D. Ashlock, deceased); USNM (Department of Entomology, U.S. National Museum of Natural History, Washington, DC); USU (Utah State University, Logan, W. J. Hanson); ZMU (Zoological Museum of the University, Helsinki, A. Jansson).

TAXONOMIC HISTORY OF *KELTONIA* AND *PSEUDATOMOSCELIS*

Poppius (1911) erected the genus *Pseudatomoscelis* to accommodate *Atomoscelis seriatus* Reuter and his new species *P. tuckeri,* which he separated from *Atomoscelis* Reuter based primarily on head structure. Van Duzee (1916), without comment, placed *Pseudatomoscelis* as a junior synonym under the genus *Psallus,* an opinion followed by Blatchley (1926), Knight (1926a, b, 1941), and Carvalho (1952, 1958, 1959). Knight (1968) reevaluated the position of *P. seriatus* and, based on the antennal spotting and clustered sericeus setae on the hemelytra, returned it to *Pseudatomoscelis,* where it has remained as the only recognized species until the present study.

Knight (1923), in recognizing that *Psallus sulphureus* Reuter was not congeneric with *Psallus* Fieber, transferred it to the genus *Reuteroscopus* Kirkaldy. Carvalho

(1958), apparently following Knight's concept of Reuter's species, synonymized *Pseudatomoscelis tuckeri* Poppius (then placed in the genus *Psallus*) with *R. sulphureus.* Kelton (1964) showed that *sulphureus,* based on genitalia and other characters, is not congeneric with other species of *Reuteroscopus* but, in cooperation with Knight, deferred taking taxonomic action. Subsequently, Knight (1966) established the genus *Keltonia* to accommodate *sulphureus,* transferred *Psallus balli* Knight to this new genus, synonymized *Psallus conspurcatus* Blatchley with *K. sulphurea,* and described the new species *K. fuscipunctata* and *K. rubrofemorata.* Kelton (1966) described the new species *K. clinopodii* and *K. knighti* and provided a revised key to species.

GENERIC RELATIONSHIPS OF *KELTONIA* AND *PSEUDATOMOSCELIS*

For this study, I have examined representatives of most New World and many Old World genera of Phylinae in search of potential relatives of *Pseudatomoscelis seriatus.* Initially, I narrowed my search to those taxa possessing dorsal spots and/or sericeus body pubescence (here defined as short, thickened, silky setae (Torre-Bueno, 1973); also referred to as moderately flattened, apically acuminate, scalelike setae by Schuh and Schwartz (1985) and Stonedahl (1990)). It soon became evident that dorsal spotting has evolved numerous times in the Phylinae, and although apomorphic for specific taxa, this character does not represent a synapomorphy for broad groups (e.g., *Atomoscelis,* some species of *Phymatopsallus* Knight and *Plagiognathus* Fieber). Even within *Pseudatomoscelis, P. seriatus* has distinct dorsal spotting, whereas its sister species *P. flora* (Van Duzee) is immaculate.

Schuh (1984), Schuh and Schwartz (1985), and Stonedahl (1990), among others, have shown that sericeus setae can be informative regarding phyline relationships. Schuh and Schwartz (1985) noted that *Pseudatomoscelis seriatus* possesses a mesially swollen, flattened, and apically acuminate, sericeus setal type shared by a number of taxa, including *Atractotomus magnicornis* (Fallén), *Campylomma verbasci* (Meyer-Dür), *Europiella stigmosa* (Uhler), and *Psallus ancorifer* (Fieber). Study of male genitalia, however, indicates that most of these taxa are not particularly close to *Pseudatomoscelis.* Most have sigmoid vesicae and the sericeus setae never appear in clusters.

Genitalia reveal that members of the genus *Keltonia,* not previously associated with *Pseudatomoscelis,* share a vesica type close to *P. seriatus.* Perusal of other characters indicates that these two genera form a sister-group relationship.

Synapomorphies that support the monophyly of *Keltonia* and *Pseudatomoscelis* are 1) a stout, C-shaped vesica, bearing a large, sickle-shaped spicule; 2) clumps or tufts of acuminate sericeus setae usually distributed over dorsum, but always present along the inner margin of the eye near the base of the antenna; 3) 1 or 2 patches of dark, bristlelike setae along inner margin of the cuneus; and 4) a large dark area on membrane near apex of cuneus.

Synapomorphies that support the monophyly of species included in *Pseudatomoscelis* are 1) a stout, C-shaped vesica, with a broad, swordlike spicule, but lacking a flattened, cuplike, apical process (as is found in *Keltonia*); 2) a stout, subapical spine on the phallotheca; 3) antennal segment II spotted; and 4) a somewhat saltatorial metafemur bearing 2 or more stout, subapical, bristlelike setae.

Synapomorphies supporting the monophyly of species placed in *Keltonia* are 1) a

stout, C-shaped vesica bearing a flattened, cuplike, apical process (spicule variable from slender to broad and from acuminate to truncate apically); 2) head, pronotum, and scutellum with a distinct mesal line of silvery sericeus setae; and 3) membrane distinctly conspurcate.

A search for an outgroup to use in helping to polarize character information proved somewhat more difficult. G. M. Stonedahl (pers. comm.) indicated to me that *Psallus biguttatus* Van Duzee appeared to share a number of attributes with *Keltonia* and *Pseudatomoscelis* that suggested some relationship. This species, obviously not belonging in the genus *Psallus,* bears the clumps or tufts of silvery sericeus setae along the inner margin of the eye near the antennal base (the minimum found in *Keltonia* and *Pseudatomoscelis*), has indications of homologous dark patches along the inner margin of the cuneus (although no specimens examined have the dark bristlelike setae found in *Keltonia* and *Pseudatomoscelis*), and there is a dark area just beyond the apex of the cuneus on the membrane. Certain other apomorphies, however, indicate that *P. biguttatus* is not congeneric with *Keltonia* and *Pseudatomoscelis* and represents a new genus, which is described as *Lineatopsallus* in this paper. Synapomorphies supporting the monophyly of the species placed in this genus include 1) a distinct fuscous line present on antennal segment II, dorsally along each femur, and along the length of all tibiae; 2) a very slender, although C-shaped, vesica that lacks a spicule separate from the primary shaft; 3) a left paramere possessing a short process basal to the left arm; and 4) a unique, apically flattened phallotheca.

SYSTEMATICS

Keltonia Knight

Keltonia Knight, 1966:590; Kelton, 1966:668; Henry and Wheeler, 1988:469. Type species: *Keltonia rubrofemorata* Knight, 1966. Original designation.

Diagnosis. Phylinae: Phylini. *Keltonia* is distinguished from all other members of the tribe Phylini by the pale body coloration (pallid, yellow, yellowish orange, to reddish orange); dorsal spots limited to the hemelytra; conspurcate hemelytral membrane; dark setal patches on inner margin of cuneus; two types of dorsal pubescence, with sericeus pubescence present in distinct clumps or tufts and often in rows along midline of head and pronotum; pale tibiae with dark spots at the bases of the spines; and the stoutly formed, weakly twisted, C-shaped vesica, with a distinct slender spicule and a cuplike, apical process.

Description. Generally elongate oval, somewhat delicate, small to medium sized, length from apex of tylus to apex of hemelytral membrane 2.36–4.20 mm; coloration ranging from pallid or white to yellow, yellowish green, yellowish orange, and reddish orange, often appearing to have a phosphorescent, velvety bloom under certain reflected lights; dorsal surface impunctate, smooth, shiny or dull, clothed with simple, semierect setae, intermixed with individual and/or tufts and rows of silvery, sericeus or scalelike setae. Head subtriangular in dorsal aspect, tylus slender, pronounced, antennal segment I not or just surpassing apex of tylus, antennal fossa or socket set anteriorly adjacent to lower half of compound eye near shallow, inner emargination, eyes with short, sparse pubescence; jugum adjacent to base of tylus with a tuft of silvery, sericeus setae, often with 2 or 3 tufts near inner margin of each eye and a narrow row along midline or meson (Figs. 45, 46, 50, 51). Rostrum extending to

metacoxae or beyond. Antenna slender, segment I shortest and thickest, II longest, III and IV most slender, combined lengths subequal to length of II. Pronotum trapeziform, unspotted, with simple, recumbent and silvery, sericeus setae. Hemelytron macropterous, surface immaculate to variously spotted—spotting ranging from evenly sprinkled, to coalescing on inner half of corium and apical area of clavus forming a dark cloud at middle, to nearly absent on pale species (Figs. 13–16, 41–43); cuneus longer than wide at base, inner margin bordering membrane with 1 or 2 darkly pigmented patches giving rise to stout, fuscous or black setae; membrane always conspurcate (dark with pale spots or pale with dark spots). Legs slender; femora slender (i.e., not saltatorial), usually with fine, brown spots; tibiae pale with brown or fuscous spots at bases of spines; claws slender, with setiform parempodia and short, quadrate, fleshy pulvilli (Figs. 48, 53). Parameres typically phyline; left paramere with 2 parallel processes, anterior (left) one short, blunt or acute, posterior (right) one long, acute, vesica extending through and resting between processes of left paramere in withdrawn position; right paramere simple, elongate oval, with a slender stemlike base. Vesica stout, C-shaped, primary body sheathlike, with a slender spicule extending to apex of sheath, and apical process bluntly rounded, shallowly cuplike, and flattened; secondary gonopore subapical.

Females are similar to males in general coloration and pubescence, but usually differ in by their larger, broader body size, proportionately smaller eyes, broader vertex, and slightly more slender 2nd antennal segment.

Remarks. *Keltonia* is most closely related to the genus *Pseudatomoscelis* based on the shared hemelytral spotting of most species, the setigerous black patches on the cuneus and paracuneus (inner, basal angle of cuneus, lacking suture), two types of pubescence including the uniquely tufted sericeus setae, spots at the bases of the tibial spines, and the stoutly formed, C-shaped vesica. Species of this genus can be separated from those of *Pseudatomoscelis* by the lack of spots on the antennae, lack of stout, black, bristlelike setae on the apical third of the femora, the slender metafemora that are never saltatorial, the distinctly conspurcate membrane, and the cuplike, apical process on the vesica. See "Phylogenetic Relationships" for further discussion.

Although *K. sulphurea* [of authors] has been placed in *Reuteroscopus* Reuter, and Knight (1966) wrote when describing *Keltonia* "a new genus near *Reuteroscopus,*" *Reuteroscopus* is not closely allied with *Keltonia* and *Pseudatomoscelis* in the tribe Phylini. Species of *Reuteroscopus* lack sericeus pubescence, spots at the bases of the tibial spines, and setigerous black cuneal spots, and the male genitalia (see Kelton, 1964) are bizarrely unique in the subfamily Phylinae and quite distinct from species in *Keltonia* and *Pseudatomoscelis.*

In the following key to species, reasonably well-preserved specimens are necessary to correctly evaluate the characters used, especially coloration, dorsal spotting, and relative position of the rostrum. Specimens prepared from alcohol tend to fade, and upon drying the natural position of the head and rostrum in relation to the body often becomes distorted.

KEY TO THE SPECIES OF *KELTONIA*

1. Hemelytral spots coalescing to form a conspurcate brown cloud or solid dark area through middle of corium and apex of clavus (Figs. 16, 42, 49) 2

– Hemelytral spots evenly distributed or absent, never forming a dark area through middle of corium and apex of clavus 6
2. Dorsum bright shiny yellow; hemelytron lacking small brown spots around solid dark area at middle; femora red to dark reddish brown; central Florida .... *rubrofemorata* Knight
– Dorsum dull, sometimes phosphorescent, yellow; hemelytra with numerous spots surrounding coalesced spots or dark cloud at middle; femora always pale, with small brown spots 3
3. Cuneus and embolium without brown setigerous spots; spots on corium nearly limited to central brown area; central Florida .... *clinopodii* Kelton
– Cuneus, embolium, and corium with distinct, brown setigerous spots 4
4. Rostrum short, extending only to metacoxae; vertex narrow, width subequal to 1.5 × dorsal width of an eye in males, 2 × in females; central and southern Mexico ..... **mexicana**, n. sp.
– Rostrum longer, extending well beyond metacoxae to base of male genital segment or ovipositor in females; vertex wider, 2.5 × or more dorsal width of an eye in males, 3 × in females 5
5. Second antennal segment distinctly longer than basal width of pronotum in males, subequal in females; spicule of vesica curved upward apically (Fig. 17); Sinaloa, Mexico .... *knighti* Kelton
– Second antennal segment less than or subequal to basal width of pronotum; spicule of vesica straight apically (Fig. 62); Massachusetts to Colorado, south through Mexico to Colombia and Venezuela .... *tuckeri* (Poppius)
6. Dorsum yellowish to pale reddish orange, cuneus contrasting red to deep reddish orange (Fig. 13); central and northern Florida .... *balli* (Knight)
– Dorsum pallid, yellow, or pale yellowish orange, cuneus never contrasting deep reddish orange 7
7. Hemelytra devoid of spots, or the few spots present hardly visible 8
– Hemelytra with numerous, evenly distributed, easily visible spots 9
8. Overall coloration pallid to dull greenish white; clavus and corium uniformly pale, without spots (cuneus and embolium sometimes with a few indistinct spots); coastal Texas .... **pallida**, n. sp.
– Overall coloration shiny, translucent yellow; clavus and corium with tiny, vague spots; Oaxaca, Mexico .... **schaffneri**, n. sp.
9. Large robust species, length 3.50 mm or more; rostrum 2 mm long or more; northern Florida .... **robusta**, n. sp.
– Smaller species, length 3.10 mm or less; rostrum 1.80 mm or less 10
10. Length of rostrum 1.70–1.80 mm; dorsum pallid to pale lemon yellow; Grand Bahama Island .... **steineri**, n. sp.
– Length of rostrum 1.60 mm or less; dorsum more greenish yellow 11
11. Length of rostrum 1.30–1.40 mm, not extending beyond base of genital segment; apex of spiculum on vesica acute (Fig. 58); Jamaica and Florida .... *sulphurea* (Reuter)
– Length of rostrum 1.45–1.60 mm, extending well beyond base of genital segment; apex of spiculum on vesica forked or bifurcate (Fig. 5); Guerrero, Mexico .... **bifurca**, n. sp.

Keltonia balli (Knight)
Figs. 1–4, 13

Psallus balli Knight, 1926b:253.
Keltonia balli: Knight, 1966:591; Kelton, 1966:670; Henry and Wheeler, 1988:469.

Diagnosis. *Keltonia balli* is distinguished from all other species of the genus by the unique multicolored dorsum (Fig. 13) and legs. The orange to brownish or reddish-orange head and pronotum and deep-orange to red-orange cuneus, contrasted by the paler areas of the corium and clavus would suggest that this species is not congeneric with others of the genus. However, the peculiarly patterned silvery, sericeus pubescence, dark cuneal spots, conspurcate membrane, and male vesica support its current generic position.

In the key, I interpret this species as lacking a conspurcate or solid cloud through the middle of the corium and apex of the clavus. Even though the apical area of the clavus is often darkened or spotted, the inner angles of the corium always remain pale.

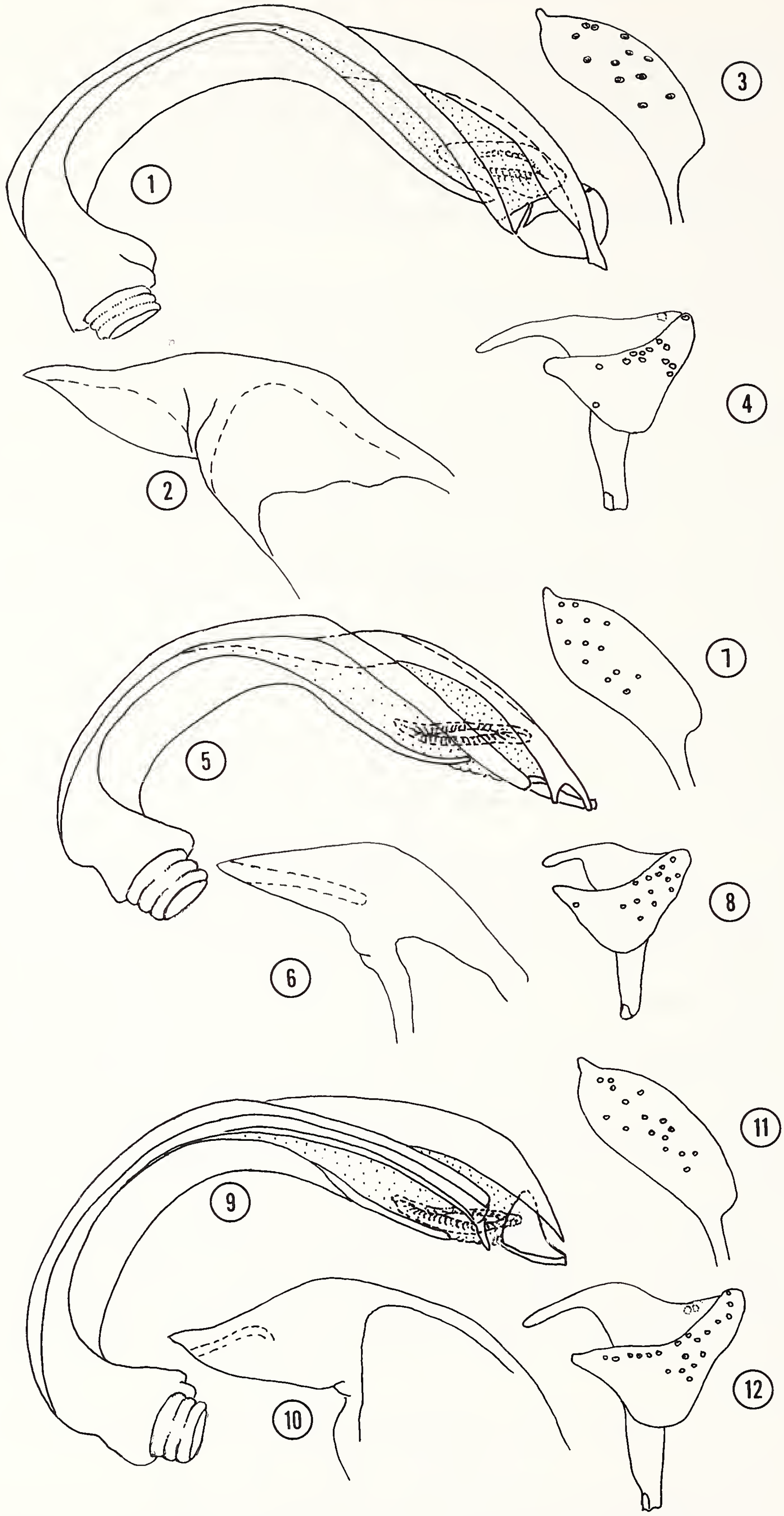
Description. Male (N = 4): Length 3.32–3.68 mm, width 1.32–1.36 mm. *Head:* Width 0.72–0.74 mm, vertex 0.32–0.34 mm. *Rostrum:* Length 1.22–1.24 mm, extending to bases of metacoxae. *Antenna:* Segment I, length 0.24–0.26 mm; II, 1.06–1.08 mm; III, 0.66–0.68 mm; IV, 0.56 mm (segment missing on remaining 3 specimens). *Pronotum:* Length 0.50–0.52 mm, basal width 1.08–1.12 mm.

Female (N = 1): Length 3.52 mm, width 1.44 mm. *Head:* Width 0.72 mm, vertex 0.36 mm. *Rostrum:* Length 1.28 mm, extending to bases of metacoxae. *Antenna:* Segment I, length 0.24 mm; II, 1.02 mm; segment III and IV missing. *Pronotum:* Length 0.52 mm, basal width 1.16 mm.

General coloration pale to dark reddish orange, dorsum with recumbent, golden-brown, simple pubescence, intermixed with sericeus setae. Head orange to brownish orange, frons with a few darker orange spots or reticulations; tufts or clumps of silvery, sericeus setae patterned as follows: 3 along inner margin of eyes (almost merging to form a broken line), 1 on either side of tylus at base, and a broken row along meson. Antenna yellowish to pale yellowish orange; setae recumbent, golden brown, length of some approaching diameter of segment. Pronotum pale reddish to brownish orange, more orange on calli; silvery sericeus setae generally scattered with fine tufts forming a fine line along meson. Scutellum and mesoscutum orange to reddish orange, with sericeus setae mostly scattered, but on unrubbed specimens forming a fine, broken line along meson. Hemelytron multicolored; base of clavus, middle of corium, and cuneal fracture pale or yellowish; apex of clavus clouded with brown to smoky brown, usually also with small brown spots; lateral and basal ½ and apex of corium pale reddish orange, cuneus bright reddish orange; surface thickly scattered with silvery sericeus setae, setae more concentrated on pale middle area of corium; membrane brown to fumate, with numerous, small, pale spots giving a conspurcate appearance, and a large, elongate spot near apex of cuneus. Ventral surface uniformly pale brownish to reddish orange. Legs pale yellowish orange; femora yellowish orange, hind femora dark, brownish to reddish orange with numerous, fine, brown spots on apical ⅔, pro- and mesofemora pale with brown spotting almost obsolete; tibiae pallid or pale yellow, pale tibial spines with brown spots at bases; claws brown.

Male genitalia: Vesica (Fig. 1); phallotheca (Fig. 2); right paramere (Fig. 3); left paramere (Fig. 4).

Specimens examined. United States—FLORIDA: 3 ♂♂, Gainesville [Alachua Co.], 8–9 Oct. 1968, F. W. Mead, at blacklight trap (FSCA, USNM); 1 ♂, Highlands Co., Archbold Biological Station, 24 Nov. 1971, S. W. Frost (PSU); 1 ♂, Marion Co., 9



Figs. 1–12. Male genitalia of *Keltonia* spp. *K. balli*: 1. Vesica. 2. Phallotheca. 3. Right paramere. 4. Left paramere. *K. bifurca*: 5–8. *K. clinopodii*: 9–12.

mi SSW Ocala, 27 VIII 1975, Drummond & Wiley (FSCA); 1 ♂ (autotype), Winter Park [Orange Co.], 25 Apr. 1940, H. T. Fernald, at light (USNM); 1 ♀ (allotype), Sanford [Seminole Co.], March 15, 1926, E. D. Ball (USNM).

Distribution. Known only from five counties in central and northern Florida.

Hosts. Unknown. The unusual orange coloration of this bug would suggest that it is cryptically colored for life suited to a plant of complementary color.

Keltonia bifurca, new species
Figs. 5–8

Diagnosis. *Keltonia bifurca* is similar to *K. robusta, K. steineri,* and *K. sulphurea* is having distinct, evenly distributed hemelytral spots. It is distinguished from *K. robusta* by the smaller size and much shorter length of the rostrum. From *K. steineri* it differs in the more greenish-yellow coloration and shorter length of the rostrum. Externally, *K. bifurca* is very much like *K. sulphurea,* but has paler brown, less distinct hemelytral spots, and the rostrum extends well beyond the base of the male genital capsule and the ovipositor in females. The bifurcate or forked spicule of the vesica (Fig. 5) is unique in the genus.

Description. Male (N = 3): Length 2.68–2.80 mm, width 1.12–1.22 mm. *Head:* Width 0.60–0.62 mm, vertex 0.30–0.32 mm. *Rostrum:* Length 1.46–1.48 mm, extending to middle of genital segment. *Antenna:* Segment I, length 0.22–0.24 mm; II, 0.86–0.90 mm; III, 0.54–0.56 mm; IV, 0.38–0.40 mm. *Pronotum:* Length 0.40–0.42 mm, basal width 0.88–0.92 mm.

Female (N = 2): Length 2.80–2.88 mm, width 1.20–1.22 mm. *Head:* Width 0.58–0.60 mm, vertex 0.30–0.34 mm. *Rostrum:* Length 1.46–1.56 mm, extending past base of ovipositor. *Antenna:* Segment I, length 0.20–0.22 mm; II, 0.84–0.90 mm; III, 0.54–0.56 mm; IV, 0.36–0.40 mm. *Pronotum:* Length 0.40–0.44 mm, basal width 0.90–0.92 mm.

General coloration yellow to greenish yellow, dorsum with semierect, golden-brown, simple setae, intermixed with silvery sericeus pubescence. Head uniformly yellow. Antenna yellowish, segment I with a subapical and subbasal, pale-brown spot or partial band, apex with 2 brown, bristlelike setae. Pronotum yellow, with semierect, golden-brown setae and scattered tufts or clumps of silvery sericeus setae. Scutellum yellow, with a few scattered clumps of silvery sericeus setae. Hemelytron yellow, somewhat translucent on some specimens, uniformly sprinkled with small, pale-brown spots, some specimens with larger brown spots along embolium and through middle of corium; thickly set with semierect, golden-brown, simple setae, intermixed with clumps of silvery sericeus setae; inner margin of cuneus with 2 patches of dark-brown, bristlelike setae; membrane dark smoky brown or fumate, broken by numerous small, pale spots, giving a conspurcate appearance, large area adjacent to apex of cuneus and just after large, solid, dark spot pale or clear. Ventral surface yellow to greenish yellow. Legs yellow; all femora sprinkled with pale-brown spots, but less so at bases; dark or fuscous tibial spines with dark-brown spots at bases, especially on metatibiae; tarsi yellow; claws brown.

Male genitalia: Vesica (Fig. 5), spiculum slender with apex forked or bifurcate; phallotheca (Fig. 6); right paramere (Fig. 7); left paramere (Fig. 8).

Type specimens. Holotype ♂: Mexico, Guerrero, 20 mi E Acapulco, July 10, 1974,

Figs. 13–16. Habitus photographs. 13. *Keltonia balli.* 14. *K. pallida.* 15. *K. robusta.* 16. *K. rubrofemorata.*

Clark, Murray, Ashe, & Schaffner (USNM). Paratypes: 2 ♂♂, 2 ♀♀, same data as for holotype (TAM, 1 USNM).

Etymology. This species is named for the bifurcate or forked apex of the spiculum on the vesica.

Distribution. Guerrero, Mexico.

Hosts. Unknown.

Keltonia clinopodii Kelton
Figs. 9–12

Keltonia clinopodii Kelton, 1966:668; Henry and Wheeler, 1988:469.

Diagnosis. *Keltonia clinopodii* most closely resembles *K. tuckeri* in the greenish- to lemon-yellow coloration and the coalesced brown spots on the central area of the hemelytron. However, it differs consistently from *K. tuckeri* in having noticeably fewer spots on the hemelytron, especially on the cuneus and at the base and lateral ½ of the corium; on many specimens of *K. clinopodii,* the coalesced hemelytral spots are almost absent except for a few at the apex of the clavus and inner angle of the corium. Also, *K. clinopodii* feeds on a mint, whereas *K. tuckeri* appears to be a composite specialist.

Description. Male (N = 10): Length 2.80–3.32 mm, width 1.12–1.28 mm. *Head:* Width 0.54–0.60 mm, vertex 0.32–0.34 mm. *Rostrum:* Length 1.42–1.54 mm, extending to base of genital capsule. *Antenna:* Segment I, length 0.20–0.22 mm; II, 0.80–0.92 mm; III, 0.54–0.56 mm; IV, 0.36–0.40 mm. *Pronotum:* Length 0.36–0.44 mm, basal width 0.82–0.96 mm.

Female (N = 10): Length 2.76–3.20 mm, width 1.08–1.28 mm. *Head:* Width 0.52–0.60 mm, vertex 0.32–0.36 mm. *Rostrum:* Length 1.42–1.54 mm, extending past base of ovipositor. *Antenna:* Segment I, length 0.20–0.22 mm; II, 0.82–0.90 mm; III, 0.50–0.52 mm; IV, 0.40–0.42 mm. *Pronotum:* Length 0.38–0.42 mm, basal width 0.86–0.98 mm.

General coloration pale greenish yellow, dorsum with contrasting brown to golden-brown simple pubescence, intermixed with silvery sericeus setae. Head pale greenish yellow. Antenna pale yellow; segment I with 2 or 3 very faint brown spots; segments III and IV becoming dusky to fuscous. Pronotum pale greenish yellow; tufts of sericeus setae as follows: 3 or 4 along lateral margin, 3 or 4 on each side of disc, and a broken row along meson. Scutellum and mesoscutum pale greenish yellow with tufts of sericeus setae set evenly across mesoscutum, middle tuft extending through length of scutellum. Hemelytron uniformly greenish yellow; clavus, embolium, and inner ½ of corium with numerous small brown spots, spots coalescing near apex of clavus and inner angle of corium forming a dark but not solid area, some specimens with spotting absent, or nearly so, on embolium and clavus and, frequently, on most of corium; silvery sericeus pubescence scattered over surface, but more distinctly concentrated along embolium and in the shape of a wide band across coalesced spotted area of middle; membrane fumate, broken by numerous pale or whitish spots appearing conspurcate, small areole and a large spot adjacent to apex of cuneus pale or whitish. Ventral surface pale yellow. Legs pale yellow; apical ½ of femora with numerous, small, brown spots; golden-brown tibial spines with distinct brown spots at bases, basal spots sometimes fading apically; claws brown.

Male genitalia: Vesica (Fig. 9); phallotheca (Fig. 10); right paramere (Fig. 11); left paramere (Fig. 12).

Specimens examined. United States—FLORIDA: 1 ♀, Alachua Co., Gainesville, 20–27 Apr. 1981, T. J. Henry, at blacklight (USNM); 2 ♂♂, 2 ♀♀ (paratypes), Highlands Co., Sebring 30-IV-1961, L. A. Kelton, on *Clinopodium* (USNM); 5 ♂♂, 3 ♀♀, Highlands Co., Archbold Biol. Stn., 20–27 Apr. 1981, T. J. Henry, at blacklight (USNM); 2 ♂♂, 5 ♀♀, Highlands Co., Rt. 27, 12 mi S Lake Placid, 20 Apr. 1981, T. J. Henry,

taken on *Satureja ashei* (USNM); 9 ♂♂, 25 ♀♀ (and nymphs), Highlands Co., Rt. 70, 2 mi W Rt. 27, nr. Archbold Biol. Stn., 20 Apr. 1982, T. J. Henry & A. G. Wheeler, Jr., taken on *Satureja ashei* (USNM); 6 ♂♂, 2 ♀♀, Marion Co., Rt. 40, 15 mi E Lynne, 24 Apr. 1984, T. J. Henry & A. G. Wheeler, Jr. (USNM); 6 ♀♀, Martin Co., 7 mi S of Okeechobee Co., Rt. 298-441, 29 Apr. 1982, T. J. Henry, on *Satureja ashei* (USNM); 9 ♂♂, 7 ♀♀ (and nymphs), Polk Co., Rt. 27, 2 mi N Frostproof, 25 Apr. 1984, T. J. Henry & A. G. Wheeler, Jr., taken on *Satureja ashei* (USNM).

Distribution. Known only from central Florida.

Hosts. Species was described from specimens collected on *Clinopodium ashei* Weatherby [Lamiaceae], thus, the specific epithet *clinopodii*. However, since that description, *ashei* has been placed in the genus *Satureja* L. A. G. Wheeler, Jr. and I have collected adults and nymphs of this species in abundance on the same host, which grows in open sandy areas in central Florida.

Keltonia knighti Kelton
Figs. 17–20

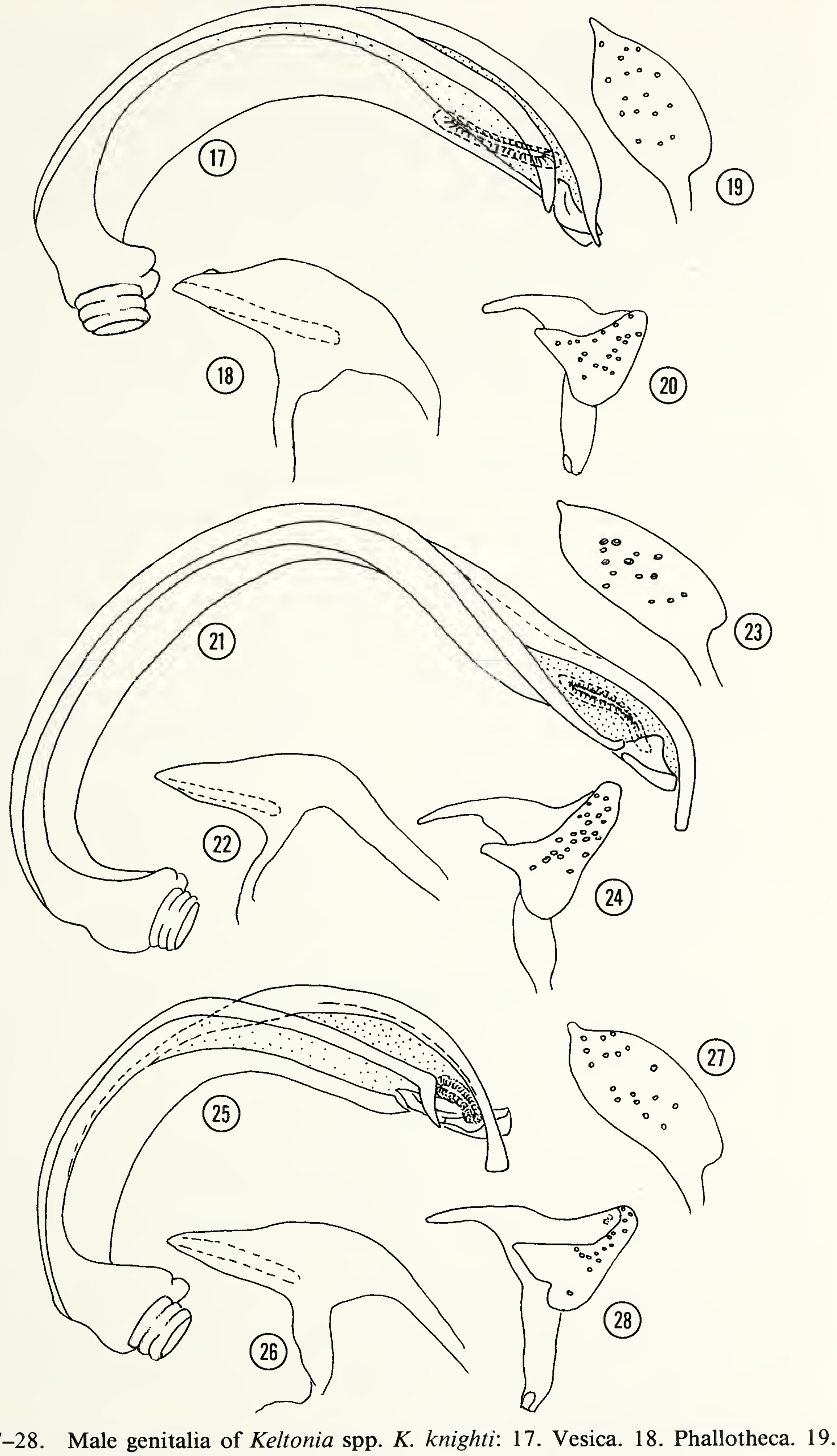
Keltonia knighti Kelton, 1966:668.

Diagnosis. *Keltonia knighti* resembles *K. mexicana* and *K. tuckeri* that also have the spots on the corium and clavus coalesced to form a large, central, brown cloud. It can be separated from *K. mexicanus* by the much broader vertex that is wider than the dorsal width of the eyes combined, and by the longer rostrum that extends well beyond the metacoxae to the base of the ovipositor or male genital segment. From *K. tuckeri* it is separated by the overall phosphorescent, yellowish-orange, dorsal coloration (rather than yellowish-green), and the 2nd antennal segment that is distinctly longer than the basal width of the pronotum in males.

Description. Male (N = 8): Length 2.80–3.12 mm, width 1.20–1.30 mm. *Head:* Width 0.56–0.60 mm, vertex 0.30–0.32 mm. *Rostrum:* Length 1.34–1.40 mm, extending beyond metacoxae to base of genital capsule. *Antenna:* Segment I, length 0.22–0.24 mm; II, 1.02–1.04 mm; III, 0.58–0.70 mm; IV, 0.44–0.46 mm. *Pronotum:* Length 0.44–0.46 mm, basal width 0.90–0.98 mm.

Female (N = 8): Length 2.72–3.08 mm, width 1.28–1.30 mm. *Head:* Width 0.58–0.60 mm, vertex 0.32–0.34 mm. *Rostrum:* Length 1.44–1.46 mm, extending to base of ovipositor. *Antenna:* Segment I, length 0.22–0.24 mm; II, 1.00–1.04 mm; III, 0.64–0.66 mm; IV, 0.42–0.52 mm. *Pronotum:* Length 0.46–0.48 mm, basal width 1.00–1.04 mm.

Coloration phosphorescent yellowish orange, dorsum with brown, semierect and recumbent, simple pubescence, intermixed with tufts of silvery sericeus setae as detailed below. Head yellowish orange. Pronotum yellowish orange, sometimes tinged with green on basal ½, tufts of silvery setae along lateral margins, through meson, and a few scattered between. Scutellum and mesoscutum yellowish orange, with scattered tufts of silvery setae. Hemelytron yellowish orange, with scattered, small, brown spots, usually over entire surface, spots coalescing across middle ⅓ of corium and across apex of clavus. Membrane smoky brown, broken by numerous pale spots and with a large pale spot adjacent to apex of cuneus and a slightly smaller one just beyond. Ventral surface uniformly pale yellow. Legs pale yellow; femora thickly



Figs. 17–28. Male genitalia of *Keltonia* spp. *K. knighti*: 17. Vesica. 18. Phallotheca. 19. Right paramere. 20. Left paramere. *K. mexicana*: 21–24. *K. pallida*: 25–28.

spotted, less so at bases; tibiae with brown spots at bases of brown spines, especially at bases; tarsi and claws pale.

Male genitalia: Vesica (Fig. 17), with spicule stout, acuminate and slightly turned up apically; phallotheca (Fig. 18); right paramere (Fig. 19); left paramere (Fig. 20).

Material examined. Holotype ♂, 10 ♂♂ and 9 ♀♀ paratypes (including designated allotype), Mexico, Sinaloa, Mazatlan, 6 Aug. 1964, L. A. Kelton (CNC; 6 paratypes in USNM).

Distribution. Known only from Sinaloa, Mexico.

Hosts. Unknown.

Keltonia mexicana, new species
Figs. 21–24

Diagnosis. *Keltonia mexicana* is most similar to *K. clinopodii* and *K. tuckeri* in having the dorsal spots on the hemelytra coalesced at the middle, but is readily distinguished by the phosphorescent, yellowish-orange coloration, the relatively large eyes, for which the combined dorsal widths are equal to or greater than the width of the vertex, and the short, stout head, which in lateral aspect, the length of an eye is equal to or greater than the remaining part of the head distally to the apex of the tylus.

Description. Male (N = 10): Length 2.90–3.40 mm, width 1.28–1.36 mm. *Head:* Width 0.62–0.64 mm, vertex 0.30–0.32 mm. *Rostrum:* Length 1.20–1.24 mm, extending to or just past apices of metacoxae. *Antenna:* Segment I, length 0.22–0.24 mm; II, 0.84–0.94 mm; III, 0.58–0.62 mm; IV, 0.44–0.46 mm. *Pronotum:* Length 0.46–0.52 mm, basal width 1.00–1.06 mm.

Female (N = 10): Length 2.92–3.48 mm, width 1.28–1.40 mm. *Head:* Width 0.60–0.64 mm, vertex 0.30–0.34 mm. *Rostrum:* Length 1.14–1.28 mm. *Antenna:* Segment I, length 0.22 mm; II, 0.78–0.94 mm; III, 0.34–0.46 mm; IV, 0.44–0.52 mm. *Pronotum:* Length 0.44–0.52 mm, basal width 0.90–1.04 mm.

General coloration phosphorescent yellowish orange, rather thickly clothed with recumbent, simple, brown setae, intermixed with tufts of silvery, sericeus setae on head, pronotum, and hemelytra. Head yellowish orange. Pronotum yellowish orange, calli somewhat more brown, with scattered tufts of silvery sericeus setae. Scutellum and mesoscutum yellowish orange, with scattered tufts of silvery sericeus setae. Hemelytron phosphorescent yellowish orange, thickly spotted with small brown spots, including cuneus, spots coalescing through middle of corium and apex of clavus to form a dark-brown clouded area, simple brown pubescence rather thick, recumbent, intermixed with scattered tufts of silvery sericeus setae, always arising from brown spots; membrane dark smoky brown, broken by numerous, small, pale spots, with larger pale areas near apex of cuneus and another slightly beyond. Ventral surface uniformly pale yellowish brown. Legs pale yellowish brown; femora with numerous small brown spots on apical halves, especially on metafemora; tibial spines dark brown, with distinct dark spots at bases, which fade apically; tarsi pale, claws brown.

Male genitalia: Vesica (Fig. 21); phallotheca (Fig. 22); right paramere (Fig. 23); left paramere (Fig. 24).

Type specimens. Holotype ♂: Mexico, Oaxaca, 2.7 mi NW El Cameron, July 13, 1971, taken at light, Clark, Murray, Hart, & Schaffner (USNM). Paratypes: 35 ♂♂, 7

♀♀, same data as for holotype (AMNH, CNC, TAM, USNM); 28 ♂♂, 10 ♀♀, 24–25 July 1973, Mastro & Schaffner, same locality as for holotype (AMNH, TAM, USNM); 2 ♂♂, 21–22 July 1974, Clark, Murray, Ashe, & Schaffner, same locality as for holotype (TAM); 2 ♂♂, Mex., Oaxaca, 11.6 mi W Jalapa de Marques, July 12, 1971, taken at light, Clark, Murray, Hart, & Schaffner (TAM); 3 ♂♂, Mex., Oaxaca, 9 mi W Tehuantepec, IV-25-65, at light, Burke, Meyer, & Schaffner (TAM); 1 ♂, 1 ♀, Mex., Oaxaca, 6 mi W Tehuantepec, July 6, 1971, taken at light, Clark, Murray, Hart, & Schaffner (TAM); 1 ♂, Mex., Oaxaca, 11 mi W Tehuantepec, July 23, 1973, Mastro & Schaffner (TAM); 1 ♂, Mex., Oaxaca, 6 mi W of Jalapa de Marques, July 23, 1973, Mastro & Schaffner, taken at light (TAM); 4 ♂♂, 6 ♀♀, Mex., Oaxaca, 16.6 mi SE Rio Hondo, July 17, 1981, Bogar, Schaffner, & Friedlander (CNC, TAM); 1 ♀, Mex., Oaxaca, 2.1 mi NW Totolapan, July 11–17, 1981, Bogar, Schaffner, & Friedlander (TAM).

Etymology. This species is named for the country in which it was discovered.

Distribution. Oaxaca, Mexico.

Hosts. Unknown.

Keltonia pallida, new species
Figs. 14, 25–28

Diagnosis. *Keltonia pallida* is one of the most distinct species in the genus and can be separated from all others by the pallid or white to pale greenish-white coloration with, at most, only a few, vague, scattered spots on the cuneus and embolium, the indistinct or absent basal cuneal (paracuneal) patch, and the weakly conspurcate membrane.

Description. Male (N = 5): Length 3.32–3.44 mm, width 1.32–1.36 mm. *Head:* Width 0.62–0.64 mm, vertex 0.36–0.38 mm. *Rostrum:* Length 1.66–1.74 mm, extending past base of genital capsule. *Antenna:* Segment I, length 0.24–0.26 mm; II, 0.98–1.00 mm; III, 0.60–0.66 mm; IV, 0.44–0.46 mm. *Pronotum:* Length 0.44–0.46 mm, basal width 0.96–1.00 mm.

Female (N = 6): Length 3.16–3.44 mm, width 1.44–1.52 mm. *Head:* Width 0.60–0.62 mm, vertex 0.40–0.42 mm. *Rostrum:* Length 1.80–1.84 mm, extending to basal ⅓ of ovipositor. *Antenna:* Segment I, length 0.24–0.26 mm; II, 1.04–1.06 mm; III, 0.58–0.60 mm; IV, 0.42–0.44 mm. *Pronotum:* Length 0.44–0.46 mm, basal width 0.98–1.02 mm.

General coloration pallid to greenish white, dorsum with recumbent, pale, simple pubescence, intermixed with silvery, sericeus setae. Head pallid. Antenna pale, segments III and IV and apical ⅓ to ½ of II dusky brown; segment I sometimes with 1 or 2 dusky spots on inner side. Pronotum pallid to greenish white, with tufted sericeus setae as follows: 3 along lateral margin, 2 or 3 on each ½ of discal area, and a broken row along meson. Scutellum and mesoscutum pallid, with a clump of sericeus setae on each side of mesoscutum and a broken row extending through middle of scutellum. Hemelytron pallid to greenish white, except for a few indistinct pale-brown spots on embolium and apical area of cuneus, set with rather thickly scattered (i.e., not in distinct tufts) sericeus setae intermixed with distinct tufts, especially along embolium and on clavus and middle of corium; apical cuneal patch distinct, but patch at base (on paracuneus) indistinct or absent; membrane white with a transverse brown streak

just past apex of cuneus, a triangular brownish cloud at apical angle, and a few scattered, brown marmorations (weakly conspurcate) through middle between areoles. Ventral surface uniformly pale greenish white. Legs pallid, with only a few, small, indistinct, brown spots at apices of metafemora; tibial spines brown, with black spots at bases on meso- and metatibiae, basal spots fading on apical ⅓ of mesotibiae, some specimens with a few spots at bases of protibial spines; claws brown.

Male genitalia: Vesica (Fig. 25); phallotheca (Fig. 26); right paramere (Fig. 27); left paramere (Fig. 28).

Type specimens. Holotype ♂: United States, Texas, Aransas Co., Ingleside, Rt. 361, 19 April 1983, T. J. Henry & A. G. Wheeler, Jr., taken on *Stemodia tomentosa* (USNM). Paratypes: 1 ♂, 2 ♀♀, same data as for holotype; 3 ♂♂, 7 ♀♀, Texas, Kleburg Co., N Padre Island, 21 April 1983, T. J. Henry & A. G. Wheeler, Jr., on *S. tomentosa* (USNM).

Etymology. This species is so named because of its overall pallid or white to pale greenish-white coloration.

Distribution. Known only from coastal Texas.

Hosts. Adults and nymphs of this species were collected and reared on *Stemodia tomentosa* (Mill.) Greenm. & Thomps. [Scrophulariaceae]. The pale coloration of this bug makes it almost impossible to detect on the pubescent, pale, greenish-white stems and foliage of this unusual prostrate plant, which grows in sandy coastal areas of the Gulf States.

Keltonia robusta, new species

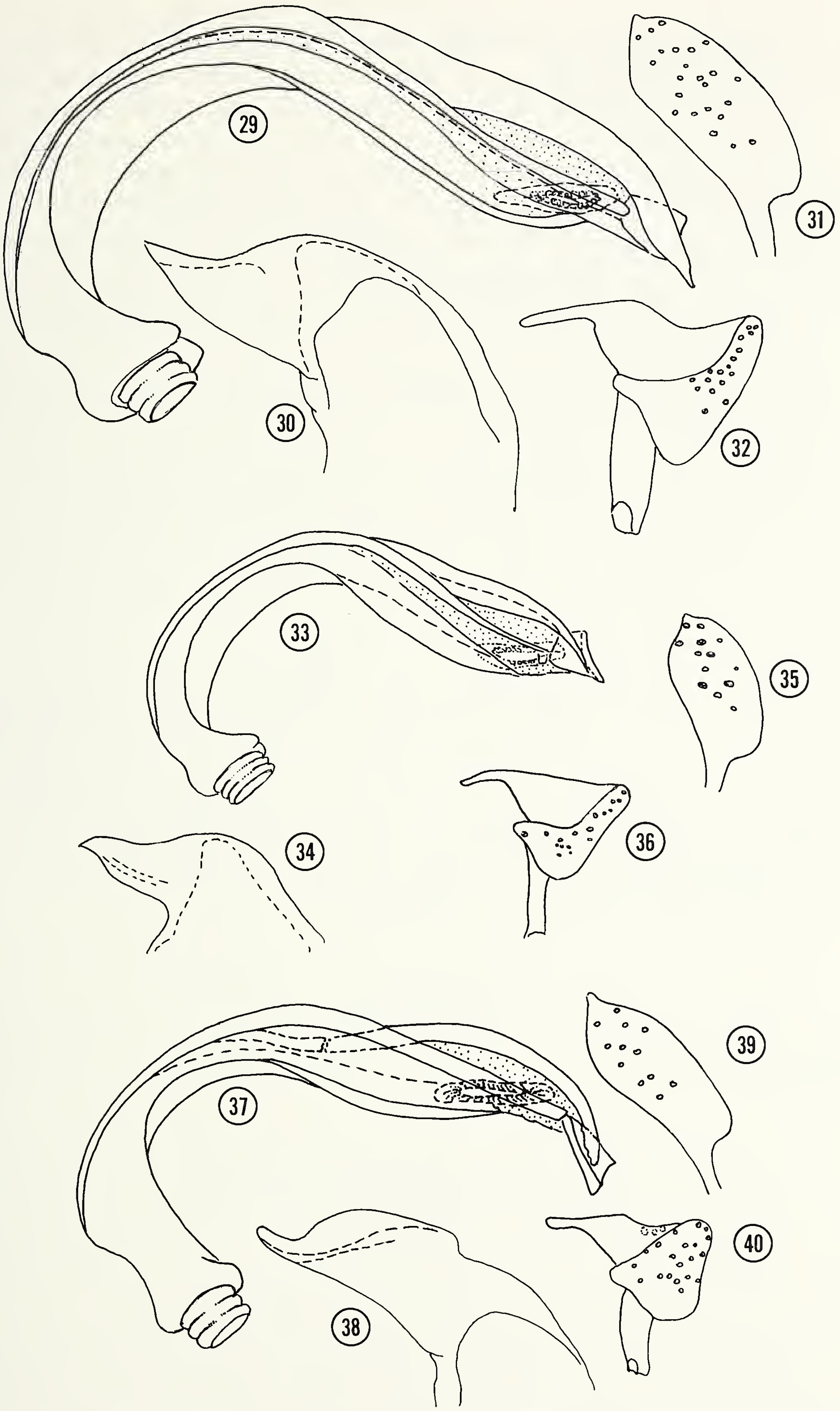
Figs. 15, 29–32

Diagnosis. *Keltonia robusta,* the largest species of the genus, is most similar to *K. sulphurea.* It can be distinguished from *K. sulphurea* by the larger size (length more than 3.50 mm vs. 3.00 mm or less for *K. sulphurea*), the smaller, more profusely sprinkled, hemelytral spots, and the longer length of the rostrum that reaches midway on the male genital capsule and base of the ovipositor in females.

Description. Male (N = 8): Length 3.52–4.20 mm, width 1.52–1.60 mm. *Head:* Width 0.68–0.70 mm, vertex 0.36–0.38 mm. *Rostrum:* Length 2.04–2.08 mm; extending midway on genital segment. *Antenna:* Segment I, length 0.24–0.30 mm; II, 1.16–1.18 mm; III, 0.68–0.74 mm; IV, 0.44–0.50 mm. *Pronotum:* Length 0.48–0.56 mm, basal width 1.16–1.24 mm.

Female (N = 10): Length 3.50–3.96 mm, width 1.52–1.56 mm. *Head:* Width 0.66–0.70 mm, vertex 0.38–0.40 mm. *Rostrum:* Length 2.04–2.20 mm; extending to base of ovipositor. *Antenna:* Segment I, length 0.24–0.26 mm; II, 1.06–1.18 mm; III, 0.68–0.76 mm; IV, 0.38–0.48 mm. *Pronotum:* Length 0.50–0.54 mm, basal width 1.16–1.20 mm.

General coloration phosphorescent yellowish green, dorsum with recumbent, golden-brown, simple pubescence, intermixed with silvery, sericeus setae. Head greenish yellow. Antenna uniformly yellow to greenish yellow, segment I sometimes with 2 pale-brown spots, segments III and IV and apical ½ of II sometimes pale, dusky brown; pubescence short, recumbent, pale golden brown. Pronotum greenish yellow, more green on discal area (posterior to calli); tufted sericeus setae finer than on head,



Figs. 29–40. Male genitalia of *Keltonia* spp. *K. robusta*: 29. Vesica. 30. Phallotheca. 31. Right paramere. 32. Left paramere. *K. rubrofemorata*: 33–36. *K. schaffneri*: 37–40.

tufted pattern somewhat irregular, setae concentrated along lateral margins, rectangularly around calli, and along meson. Scutellum and mesoscutum greenish yellow, middle of mesoscutum with a large tuft of sericeus setae at middle, remaining surface with scattered (i.e., not tufted), sericeus setae. Hemelytron yellowish to greenish yellow, thickly and uniformly speckled with tiny, pale-brown spots more concentrated in the central area of hemelytron (on clavus and inner ½ of corium) but not coalescing to form a solid brown area; sericeus setae evenly, but thickly, scattered on embolium, corium, clavus, and cuneus; membrane yellowish brown with numerous pale or whitish spots appearing conspurcate, veins brownish, paler apically. Ventral surface uniformly yellowish to greenish yellow. Legs pale yellow; metafemora uniformly and finely brown spotted, pro- and mesofemora more sparsely spotted; tibial spines brown with brown spots at bases.

Male genitalia: Vesica (Fig. 29); phallotheca (Fig. 30); right paramere (Fig. 31); left paramere (Fig. 32).

Type specimens. Holotype ♂: United States, Florida, Franklin Co., Carrabelle, 4 May 1981, T. J. Henry, taken on *Conradina canescens* (USNM). Paratypes: 10 ♂♂, 17 ♀♀, same data as for holotype (FSCA, USNM); 3 ♀♀, Florida, Franklin Co., 5 mi W Carrabelle, 4 May 1981, T. J. Henry, on *C. canescens* (USNM); 2 ♂♂, 11 ♀♀, Florida, Franklin Co., Rt. 98, Carrabelle, 1 May 1984, T. J. Henry & A. G. Wheeler, Jr., on *C. canescens*; 12 ♂♂, 2 ♀♀, Florida, Gulf Co., Rt. 30, 8 mi S Port St. Joe on St. Joe Peninsula, 1 May 1984, T. J. Henry & A. G. Wheeler, Jr., on *C. canescens* (FSCA, USNM); 13 ♂♂, 11 ♀♀, Florida, Liberty Co., Rt. 12 & Jct. 271, 6 mi N Bristol, 2 May 1984, T. J. Henry & A. G. Wheeler, Jr., on *C. canescens*; 5 ♂♂, 10 ♀♀ (and nymphs), Florida, Okaloosa Co., Niceville, Rt. 20, 9 May 1981, T. J. Henry, on *C. canescens*; 6 ♂♂, 14 ♀♀, Florida, Okaloosa Co., Niceville, 9 May 1982, T. J. Henry, on *C. canescens.*

Etymology. This species is so named because of its relatively large, robust size.

Distribution. Known only from the panhandle region of Florida.

Host. Nymphs and adults were abundant on and apparently are restricted to *Conradina canescens* (Torr. and Gray) Gray [Lamiaceae].

Keltonia rubrofemorata Knight
Figs. 16, 33–36

Keltonia rubrofemorata Knight, 1966:590; Kelton, 1966:670; Henry and Wheeler, 1988:469.

Diagnosis. *Keltonia rubrofemorata* is one of the most unusual species of the genus in having the dorsal surface bright shiny yellow to yellowish green and lacking the numerous hemelytral tufts of silvery sericeus setae found on most other species. In addition, the distinct hemelytral spotting prevalent in other species of *Keltonia* is replaced by a large, solid, centrally located, fuscous area that is clothed only with relatively slender sericeus setae (i.e., not distinct tufted patches), and the head, first antennal segments, and femora are profusely marked with red.

Description. Male (N = 10): Length 2.40–2.80 mm, width 0.92–1.08 mm. *Head:* Width 0.54–0.56 mm, vertex 0.30–0.32 mm. *Rostrum:* Length 1.04–1.08 mm, extending to apices of metacoxae, not quite reaching genital capsule. *Antenna:* Segment I, length 0.16–0.20 mm; II, 0.68–0.70 mm; III, 0.44–0.50 mm; IV, 0.36–0.40 mm. *Pronotum:* Length 0.32–0.36 mm, basal width 0.80–0.82 mm.

Female (N = 10): Length 2.36–2.84 mm, width 0.92–1.12 mm. *Head:* Width 0.52–0.56 mm, vertex 0.30–0.32 mm. *Rostrum:* Length 0.92–1.00 mm, extending to apices of metacoxae. *Antenna:* Segment I, length 0.18–0.22 mm; II, 0.68–0.76 mm; III, 0.44–0.50 mm; IV, 0.34–0.36 mm. *Pronotum:* Length 0.32–0.36 mm, basal width 0.78–0.86 mm.

General coloration shiny yellow to yellowish green, marked with red and fuscous or black; dorsum sparsely clothed with simple brown pubescence, intermixed with silvery sericeus setae limited to head and central area of hemelytra. Head yellowish green, with ventral surface, tylus, and transverse reticulate pattern on frons red, with recumbent, simple, golden-brown setae and a silvery sericeus, setal patch on either side of tylus at base. Antenna generally yellowish to yellowish brown; segment I red, segments III and IV fuscous; on some specimens, all segments red or tinged with red, segment II on pale specimens with apical ¼ frequently red tinged; pubescence, simple, short, recumbent, golden brown. Pronotum uniformly yellowish green, setae simple. Hemelytron shiny yellowish green, with a large, fuscous, circular area encompassing apical ½ of clavus and inner angle of corium, sometimes with edges fading and separating into small spots, darkened area scattered with fine, silvery, sericeus setae (i.e., not forming tufts), cuneus with a black spot at middle of margin bordering membrane; membrane black, with a large pale spot near apex of cuneus and sprinkled with pale or white spots throughout most of central area. Ventral surface uniformly yellowish green. Legs: Coxae yellowish green, often strongly tinged with red; femora red to fuscoreddish, apices pale; tibiae yellowish, sometimes tinged with red at bases, tibial spines pale with darker basal spots very faint and limited to basal halves; claws pale brown.

Male genitalia: Vesica (Fig. 33); phallotheca (Fig. 34); right paramere (Fig. 35); left paramere (Fig. 36).

Specimens examined. United States—FLORIDA: 1 ♂, 1 ♀ (paratypes), [Highlands Co.] Sebring, 30-IV-1961, L. A. Kelton, on *Polygonella* (USNM); 27 ♂♂, 19 ♀♀, Polk Co., Rt. 27, 2 mi N Frostproof, 25 April 1984, T. J. Henry and A. G. Wheeler, Jr., taken on *Polygonella myriophylla* (PDA, USNM).

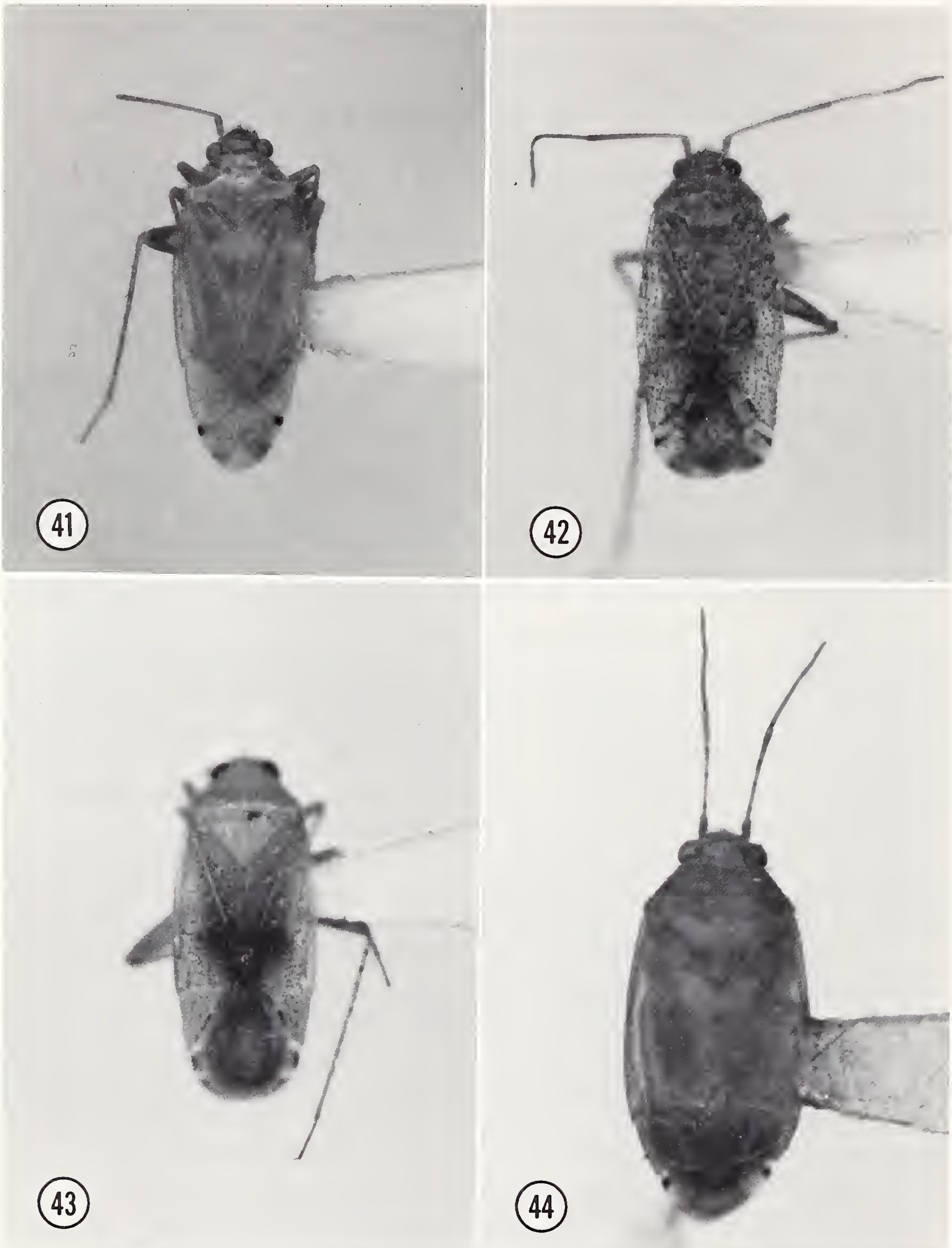
Distribution. Known only from the scrub pine/oak region of central Florida.

Hosts. Knight (1966) described this species from *Polygonella myriophylla* (Small) Horton [Polygonaceae]. A. G. Wheeler, Jr. and I also collected nymphs and adults of this attractive species in abundance on *P. myriophylla* growing on sandy hillsides along Rt. 1 a few miles north of where L. A. Kelton collected the type series.

Keltonia schaffneri, new species
Figs. 37–41

Diagnosis. *Keltonia schaffneri* is readily distinguished by the uniformly translucent-yellow coloration, indistinct, brown hemelytral spots (appear absent under low magnifications), and the absence of dark cuneal patches (repesented at most only by small, vague, brown spots and slightly darker brown setae) present in nearly all other species of *Keltonia* and *Pseudatomoscelis.*

Description. Male (N = 10): Length 2.60–2.88 mm, width 1.18–1.20 mm. *Head:* Width 0.54–0.56 mm, vertex 0.30–0.32 mm. *Rostrum:* 1.18–1.20 mm, extending



Figs. 41–44. Habitus photographs. 41. *Keltonia schaffneri.* 42. *K. sulphurea.* 43. *K. tuckeri.* 44. *Pseudatomoscelis flora.*

past metacoxae to base of genital segment in most specimens. *Antenna:* Segment I, length 0.18–0.20 mm; II, 0.82–0.86 mm; III, 0.46–0.48 mm; IV, 0.32–0.36 mm.

Female (N = 10): Length 2.74–3.04 mm, width 1.14–1.16 mm. *Head:* Width 0.52–0.54 mm, vertex 0.28–0.30 mm. *Rostrum:* 1.10–1.20 mm, extending to base of

ovipositor. *Antenna:* Segment I, length 0.20–0.22 mm; II, 0.80–0.82 mm; III, 0.46–0.50 mm; IV, 0.30–0.32 mm. *Pronotum:* Length 0.38–0.40 mm, basal width 0.84–0.86 mm.

General coloration pale shiny yellow, dorsum with semierect, pale or yellow, simple setae, intermixed with silvery sericeus setae. Head shiny yellow, sometimes with a dusky brown patch at inner posterior margin of each eye. Antenna uniformly yellow. Pronotum uniformly, shiny yellow, sometimes paler across disc behind calli; sericeus setae scattered singly or in tufts of 2 or more. Scutellum and mesoscutum yellow with a few sericeus setae. Hemelytron shiny yellow, becoming translucent along embolium, middle of corium, claval commissure, and at base and apex of cuneus, set with indistinct, pale-brown spots on clavus, corium, and cuneus; distinct setigerous fuscous patches absent on inner margin of cuneus, represented at most by only small pale-brown spots and slightly darker setae; clothed with pale-yellow, simple setae, intermixed with scattered individual or small tufts of 2–3 sericeus setae. Membrane smoky brown, broken by pallid or whitish spots, some areas becoming almost entirely pallid, lateral margin just past apex of cuneus with a large fuscous spot. Ventral surface uniformly yellow. Legs yellow; apical half of metafemur sparsely set with tiny, scattered, brown spots; tibial spines pale brown with brown spots at bases, basal spots fading apically; claws pale brown.

Male genitalia: Vesica (Fig. 37); phallotheca (Fig. 38); right paramere (Fig. 39); left paramere (Fig. 40).

Type specimens. Holotype ♂: Mexico, Oaxaca, 10 mi E Totolapan, elev. 4,000 ft, 20 July 1987, Kovarik & Schaffner (USNM). Paratypes: 10 ♂♂, 15 ♀♀, same data as for holotype (TAM, USNM); 4 ♀♀, Mexico, Oaxaca, 11 mi W Tehuantepec, 23 July 1973, Mastro & Schaffner (TAM, USNM); 1 ♀, Mexico, Sinaloa, Mazatlan, 16–18 July 1964, L. A. Kelton (CNC).

Etymology. This species is named in honor of its primary collector Joseph C. Schaffner (TAM), who also furnished more than 700 of the specimens used in this study.

Distribution. Oaxaca and Sinaloa, Mexico.

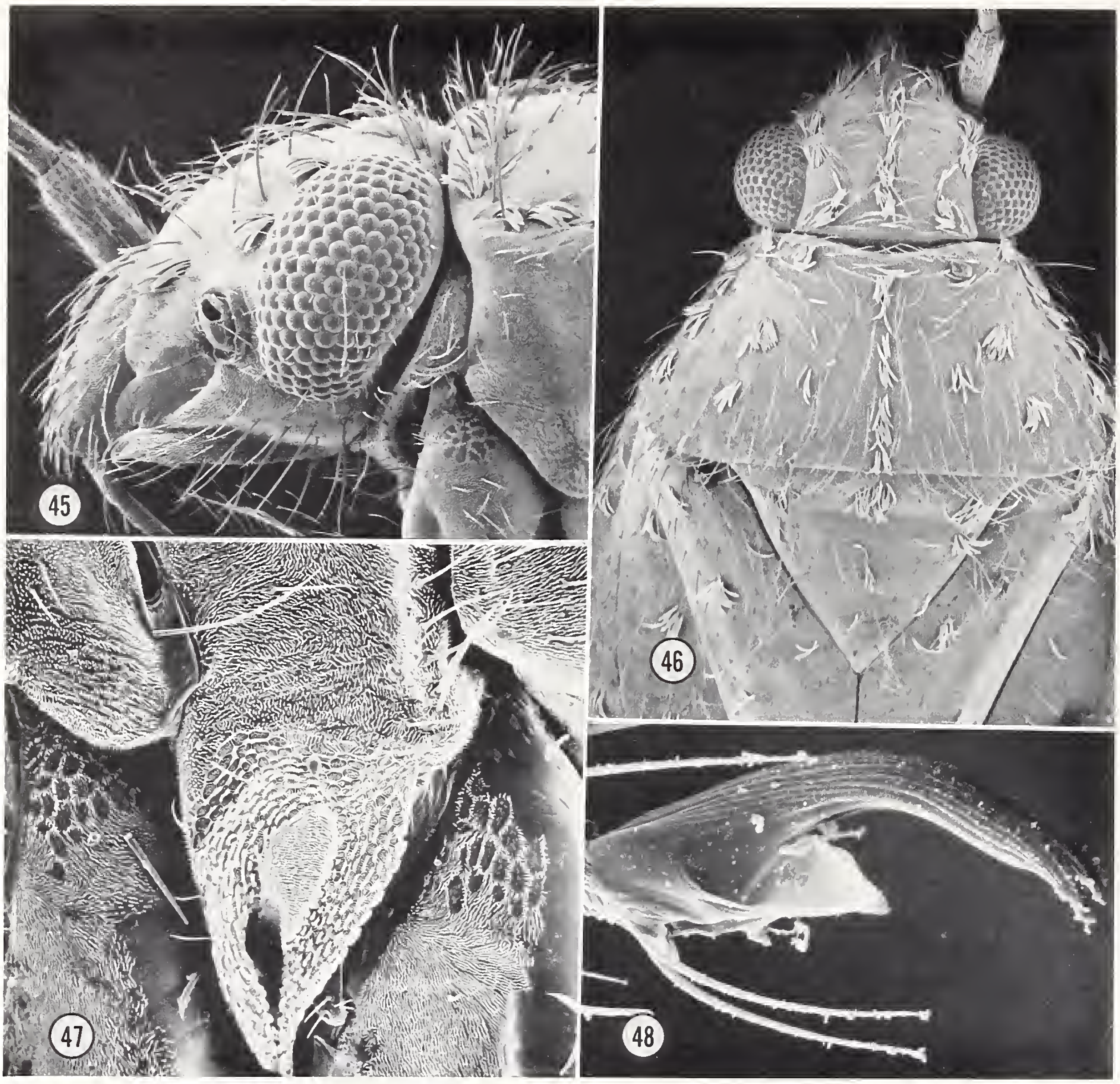
Host. Unknown.

Keltonia steineri, new species
Figs. 54–57

Diagnosis. *Keltonia steineri* belongs to the group of species that lacks the coalesced brown cloud on the middle of the hemelytron. It is most similar to *K. sulphurea* in having uniformly sprinkled, small, brown spots on the hemelytra, but is distinguished by the creamier or more "delicate" yellow coloration, and the much longer rostrum that extends well onto the male genital capsule and past the base of the ovipositor in females.

Description. Male (N = 2): Length 2.80–3.08 mm, width 1.10–1.18 mm. *Head:* Width 0.60–0.64 mm, vertex 0.32–0.34 mm. *Rostrum:* Length 1.74–1.80 mm, extending well past metacoxae to base of genital segment or beyond. *Antenna:* Segment I, length 0.22–0.24 mm; II, 0.96–0.98 mm; III, 0.54–0.60 mm; IV, 0.42–0.44 mm. *Pronotum:* Length 0.42–0.44 mm, basal width 0.90–0.92 mm.

Female (N = 1): Length 2.92 mm, width 1.18 mm. *Head:* Width 0.58 mm, vertex



Figs. 45–48. SEM micrographs of *Keltonia sulphurea*: 45. Lateral aspect of head (145×). 46. Dorsal aspect of head and pronotum (77.8×). 47. Ostiolar opening and evaporative area (285×). 48. Pretarsal structure.

0.34 mm. *Rostrum:* Length 1.80 mm, extending well beyond base of ovipositor. *Antenna:* Segment I, length 0.22 mm; II, 0.94 mm; III, 0.56 mm; IV, 0.40 mm. *Pronotum:* Length 0.40 mm, basal width 0.88 mm.

General coloration very pale to lemon yellow, with erect and semierect brown setae on dorsum, intermixed with fine tufts of silvery sericeus setae. Head pale lemon yellow. Pronotum pale lemon yellow (bright lemon yellow sometimes fading in dried specimens), with a distinct row of sericeus setae along meson, a few broken tufts along lateral margins and scattered through middle. Scutellum and mesoscutum pale lemon yellow, with scattered tufts of sericeus setae. Hemelytron very pale yellow, with evenly scattered, small, brown spots over entire surface, thickly set with erect and semierect dark-brown simple setae, sparsely intermixed with fine tufts of silvery sericeus setae. Membrane smoky brown, broken by numerous small pale spots, with a large clear spot near apex of cuneus and another just beyond; veins pale. Ventral surface uniformly pale yellow. Legs pale to very pale yellow; femora thickly speckled

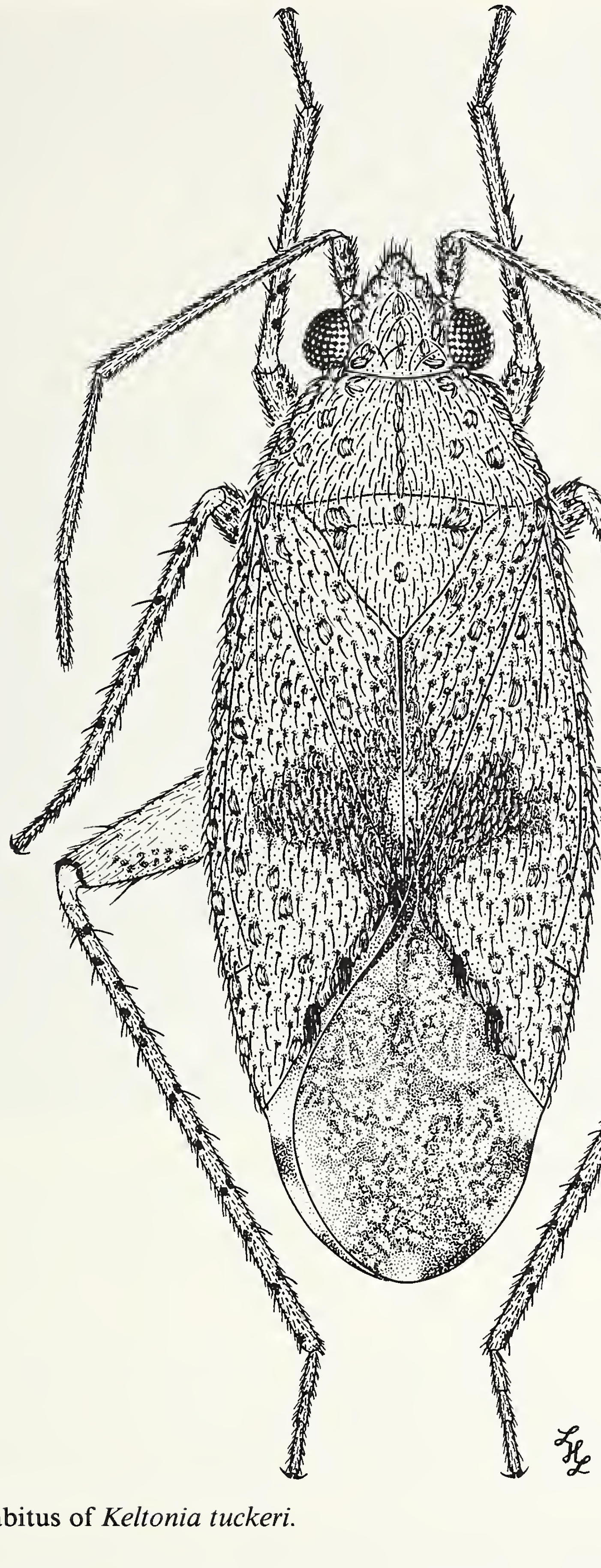


Fig. 49. Habitus of *Keltonia tuckeri.*

with small pale-brown spots on apical ⅔; tibiae with distinct dark-brown spots at bases of dark-brown to black spines; tarsi and claws pale.

Male genitalia: Vesica (Fig. 54); phallotheca (Fig. 55); right paramere (Fig. 56); left paramere (Fig. 57).

Etymology. This species is named in honor of Warren E. Steiner (USNM), who collected this attractive new mirid.

Type specimens. Holotype ♂: Grand Bahama Island, Xanadu Beach, 23 June 1987, W. E. Steiner, M. J. & R. Molineaux (USNM). Paratypes: 1 ♂, 1 ♀, same data as for holotype (USNM).

Distribution. Known only from Grand Bahama Island.

Host. Unknown.

Keltonia sulphurea (Reuter)
Figs. 42, 45–48, 58–61

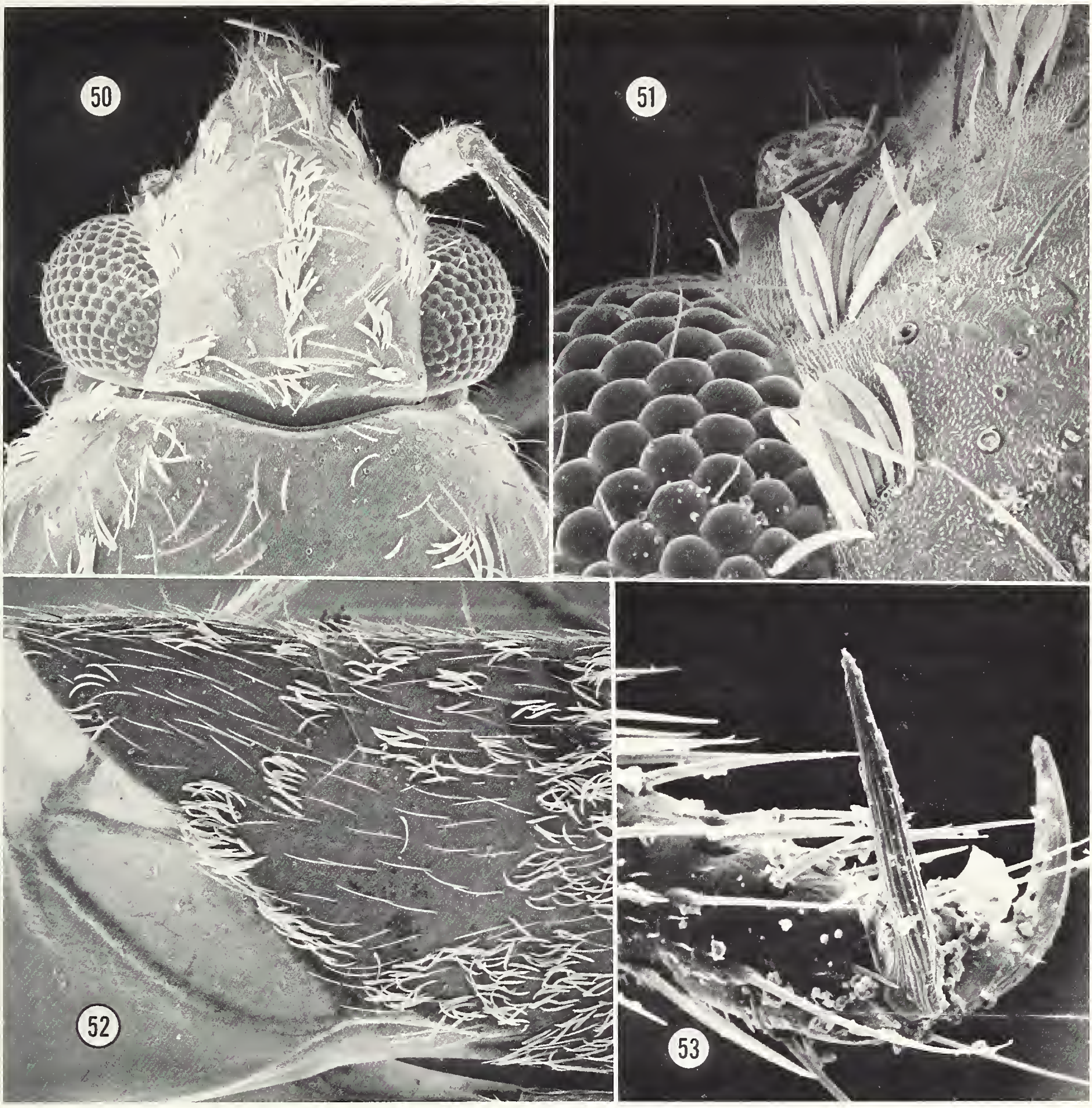
Psallus sulphureus Reuter, 1907:23; Van Duzee, 1907:27, 1909:183 (in part).
Apocremnus sulphureus: Barber, 1914:500 (in part?).
Reuteroscopus sulphureus: Knight, 1923:462 (in part); Blatchley, 1926:951 (in part); Knight, 1941:49 (in part); Carvalho, 1958:138 (in part).
Psallus conspurcatus Blatchley, 1928:16; Blatchley, 1930:66 (synonymized under *sulphurea* of authors by Knight, 1966:591). **NEW SYNONYMY.**
Keltonia fuscipunctata Knight, 1966:591; Kelton, 1966:670. **NEW SYNONYMY.**
Keltonia conspurcata: Knight, 1966:591.
Keltonia sulphurea: Knight, 1966:590 (in part); Kelton, 1966:668 (in part); Henry and Wheeler, 1988:469 (in part).

Diagnosis. *Keltonia sulphurea* belongs to the group of species possessing a uniformly brown-speckled hemelytron lacking a coalesced, central, brown area. It differs from *K. robusta* in the smaller size (length less than 3.20 mm vs. 3.50 mm or longer in *K. robusta*), the much shorter length of the rostrum that extends only just beyond the apices of the metacoxae, the larger, more distinct and uniformly distributed spots and more distinctly clumped sericeus on the hemelytra. From *K. steineri* it is distinguished by the greenish-yellow coloration, and more dense hemelytral spotting and shorter rostrum. Externally, this species is much like *K. bifurca,* but has slightly larger, more distinct hemelytral spots and the rostrum does not extend beyond the male genital capsule or the ovipositor in females.

Description. Male (N = 10): Length 2.88–3.12 mm, width 1.25–1.28 mm. *Head:* Width 0.56–0.58 mm, vertex 0.30–0.32 mm. *Rostrum:* Length 1.30–1.36 mm, extending to base of genital segment. *Antenna:* Segment I, length 0.20–0.22 mm; II, 0.86–0.92 mm; III, 0.50–0.52 mm; IV, 0.42–0.44 mm. *Pronotum:* Mesal length 0.40–0.42 mm, basal width 0.86–0.90 mm.

Female (N = 10): Length 2.88–3.16 mm, width 1.24–1.28 mm. *Head:* Width 0.56–0.58 mm, vertex 0.32–0.34 mm. *Rostrum:* Length 1.28–1.32 mm, extending to base of ovipositor. *Antenna:* Segment I, length 0.22–0.24 mm; II, 0.86–1.02 mm; III, 0.50–0.52 mm; IV, 0.40–0.44 mm. *Pronotum:* Length 0.40–0.42 mm, width 0.86–0.92 mm.

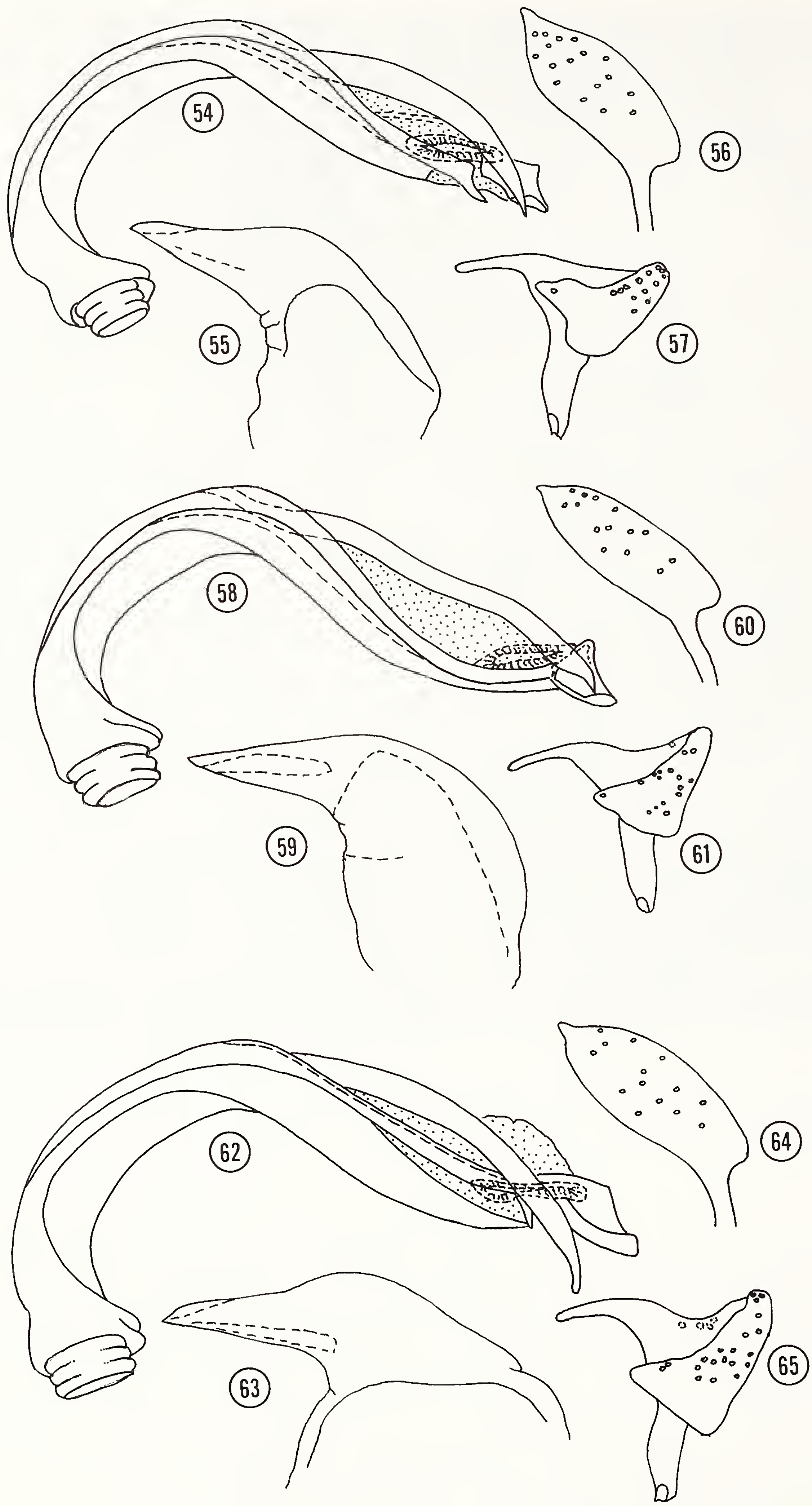
General coloration phosphorescent greenish yellow, dorsum with semierect, golden-brown, simple setae, intermixed with silvery sericeus pubescence. Head (Fig. 45) uniformly greenish yellow. Antenna yellowish, with a few pale-brown spots on segment I, general pubescence short, recumbent, segment I with 2 larger bristlelike setae. Pronotum (Fig. 46) greenish yellow; sericeus setae as follows: 3 clumps on lateral



Figs. 50–53. SEM micrographs of *Keltonia tuckeri*: 50. Dorsal aspect of head (108×). 51. Cluster of sericeus setae along inner margin of eye (384×). 52. Hemelytral pubescence, including setal patches along inner margin of cuneus (90.9×). 53. Pretarsal structure (956×).

margin, 2 on anterior and posterior margins, and a broken row along meson. Scutellum uniformly greenish yellow with 3 clumps of sericeus setae across base. Hemelytron greenish yellow, uniformly sprinkled with small, distinct, brown, setigerous spots, the larger spots bearing a patch of silvery sericeus setae, inner margin of cuneus with 2 dark-brown or black spots bearing dark bristlelike setae; membrane brownish black or fumate, broken by numerous pale or whitish spots giving a conspurcate appearance. Ventral surface uniformly greenish yellow; ostiole (Fig. 47). Legs greenish yellow; all femora with pale-brown spots on apical ⅔; tibiae with distinct dark-brown spots at bases of brown spines; tarsi yellow, claws (Fig. 48) brown.

Male genitalia: Vesica (Fig. 58); phallotheca (Fig. 59); right paramere (Fig. 60); left paramere (Fig. 61).



Figs. 54–65. Male genitalia of *Keltonia* spp. *K. steineri*: 54. Vesica. 55. Phallotheca. 56. Right paramere. 57. Left paramere. *K. sulphurea*: 58–61. *K. tuckeri*: 62–65.

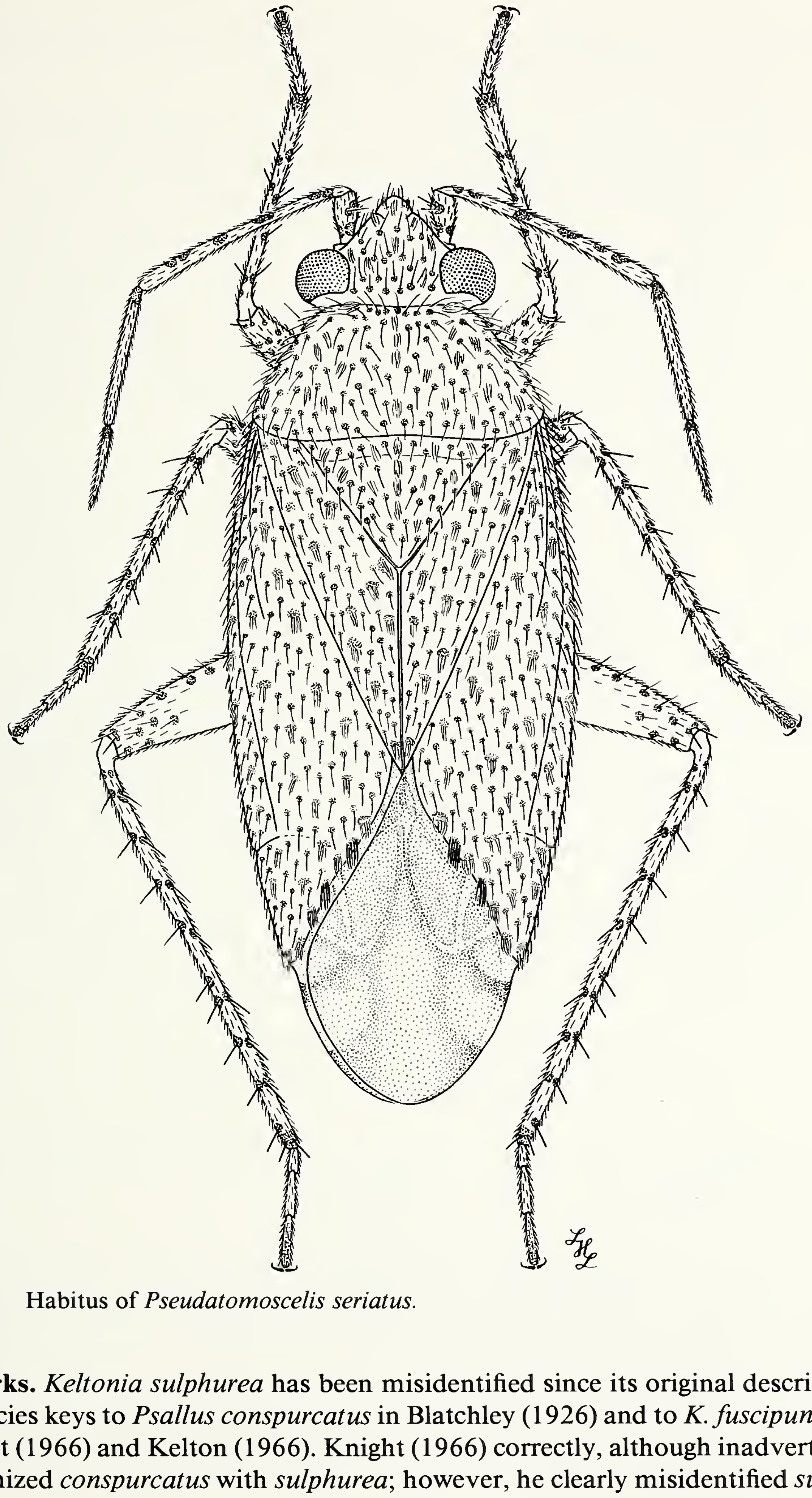


Fig. 66. Habitus of *Pseudatomoscelis seriatus.*

Remarks. *Keltonia sulphurea* has been misidentified since its original description. This species keys to *Psallus conspurcatus* in Blatchley (1926) and to *K. fuscipunctatus* in Knight (1966) and Kelton (1966). Knight (1966) correctly, although inadvertently, synonymized *conspurcatus* with *sulphurea*; however, he clearly misidentified *sulphu-*

rea, as is indicated by his description of *K. fuscipunctata.* Both are junior synonyms of *K. sulphurea.* All records of *K. sulphurea* outside Jamaica and Florida, and most within Florida, are misidentifications of *K. tuckeri.*

Type designations. No primary type has been selected from the syntype series used by Reuter (1907) in describing this species. Therefore, for nomenclatural stability, I here designate the top specimen, a male, of 3 on separate triangular points, all attached to the same pin, as the lectotype. Label data as follows: Label 1, "Kingston, Ja., Apr. 06"; 2, "Kingston, Ja., Apr. 06 [identical to label 1]"; 3, "Van Duzee Collector"; 4, "Van Duzee Collector [identical to label 3]"; 5, "24"; 6, "Mus. Zool. H:fors, Spec. typ. No. 9908, *Psallus sulphureus* Reut."; 7 (here added), "Lectotype: ♂, #1 [paralectotypes: ♀♀, # 2 & 3] *Psallus sulphureus* Reuter, by T. J. Henry." In addition, 3 other specimens, 1 male and 2 females, are attached to two pins with the same locality and collectors data and are considered paralectotypes. All specimens studied, except 1 male and 1 female (USNM), deposited in ZMU.

Other specimens examined. United States—FLORIDA: 1 ♂ (holotype of *P. conspurcatus* Blatchley), Royal Palm Park [Collier Co.], 18 April 1927, W. S. Blatchley (PU); 1 ♀ (paratype of *K. fuscipunctata*), Homestead [Dade Co.], July 19, 1939, P. Oman coll. (USNM); 5 ♂♂, 1 ♀, Gulf Co., Rt. 30, 8 mi S Port St. Joe on St. Joe Peninsula, 1 May 1984, T. J. Henry & A. G. Wheeler, Jr., on *Pluchea purpurescens* (USNM); 1 ♂, Highlands Co., Lake Placid, Archbold Biol. Stn., 19 Apr. 1982, T. J. Henry & A. G. Wheeler, Jr., at blacklight (USNM); 9 ♂♂, 9 ♀♀ (and nymphs), Liberty Co., 1.5–4 mi S Bristol, Co. Rd. 379, 7–8 May 1981, T. J. Henry, taken on *Pluchea* sp. (USNM); 6 ♂♂, 7 ♀♀, Liberty Co., Bristol, 1.5–3.0 mi S Bristol, Co. Rd. 379, 7 May 1982, T. J. Henry, taken on *Pluchea purpurescens* (USNM); 1 ♂ (holotype of *K. fuscipunctata*), [Seminole Co.] Sanford, 15 May 1926, E. D. Ball (USNM); 1 ♂ (paratype of *K. fuscipunctata*), [Volusia Co.], New Smyrna, June 1926, E. D. Ball (CNC); 1 ♀ (allotype of *K. fuscipunctata* Knight), [county?] St. John's Bluff, V-8-1927, E. D. Ball (USNM).

Distribution. Known only from Jamaica and the United States (Florida).

Hosts. No hosts have been recorded in the literature. I have collected adults and nymphs on *P. purpurescens* (Sw.) DC. [Asteraceae] in the panhandle region of Florida.

Keltonia tuckeri (Poppius), **Revised Status and New Combination**

Figs. 43, 49–53, 62–65,74

Pseudatomoscelis tuckeri Poppius, 1911:86 (synonymized with *sulphurea* by Carvalho, 1958:138).

Apocremnus sulphureus: Barber, 1914:500 (in part).

Psallus tuckeri: Van Duzee, 1916:46; Van Duzee, 1917:407.

Reuteroscopus sulphureus: Knight, 1923:462 (in part); Blatchley, 1926:951 (in part); Knight, 1927:36 (in part); Watson, 1928:40; Knight and McAtee, 1929:6; Knight, 1941:48 (in part); Froeschner, 1949:161 (in part); Carvalho, 1958:138 (in part); Kelton, 1964:1421 (in part).

Keltonia sulphurea: Knight, 1966:590, 591 (in part); Kelton, 1966:668, 670 (in part); Wheeler et al., 1983:136; McPherson et al., 1983:37; Snodgrass et al. 1984:846; Henry and Wheeler, 1988:469 (in part).

Keltonia sulphureus [*sic*]: Henry and Smith, 1979:213.

Diagnosis. *Keltonia tuckeri* belongs to the group of species having the hemelytral spots coalesced at the middle of the corium and apex of the clavus. It is distinguished from *K. mexicana* by the much longer rostrum, broader vertex, and shorter, more compact vesica. From *K. clinopodii* it is separated by the much more profusely spotted hemelytra and larger, dark area at the middle; *K. clinopodii* has the spots restricted to area immediately surrounding the small dark area at the middle of the hemelytra. From *K. knighti* is can be separated by the shorter 2nd antennal segment and the straight, apically acute spiculum.

Description. Male (N = 10): Length 3.00–3.40 mm, width 1.20–1.36 mm. *Head:* Width 0.62–0.64 mm, vertex 0.34–0.36 mm. *Rostrum:* Length 1.44–1.48 mm, extending past metacoxae nearly to genital capsule. *Antenna:* Segment I, length 0.20–0.24 mm; II, 0.94–1.06 mm; III, 0.58–0.62 mm; IV, 0.40–0.42 mm. *Pronotum:* Length 0.42–0.46 mm, basal width 0.96–1.02 mm.

Female (N = 10): Length 2.88–3.36 mm, width 1.20–1.24 mm. *Head:* Width 0.60–0.62 mm, vertex 0.32–0.34 mm. *Rostrum:* Length 1.40–1.52 mm, extending onto basal ¼ of ovipositor. *Antenna:* Segment I, length 0.20–0.22 mm; II, 0.90–1.04 mm; III, 0.60–0.68 mm; IV, 0.40–0.42 mm. *Pronotum:* Length 0.42–0.44 mm, basal width 0.90–0.96 mm.

General coloration phosphorescent, greenish yellow, often fading to yellow or yellowish-orange in preserved specimens, dorsum with semierect brown to golden-brown, simple setae, intermixed with silvery sericeus setae. Head (Figs. 50, 51) greenish yellow. Antenna yellowish, segment I with a few vague brown spots on inner surface; all segments with recumbent pale-brown setae, segment I with 3 long, brown, bristlelike setae. Pronotum greenish yellow; sericeus setae as follows: scattered patches along lateral margins and a distinct row, sometimes broken, along meson. Scutellum greenish yellow, with 3 sericeus patches across base and a broken row, often rubbed, along meson. Hemelytron greenish yellow, with small brown setigerous spots over entire surface, but sometimes fading basally on clavus and corium, spots coalescing at apex of clavus and corium to form a large, often nearly solid, brown area; patches of silvery sericeus setae (Fig. 74) scattered, but always arising from brown spots, sericeus setae on central brown area more scattered (rather than distinct patches) but dense; inner margin of cuneus (Fig. 52) and corium with a distinct dark patch bearing dark, bristlelike setae; membrane fumate, broken by numerous pale spots, appearing conspurcate, area just beyond apex of cuneus with a large fuscous spot, followed by a larger pale area. Ventral surface uniformly greenish yellow. Legs yellowish; apical halves of femora with fine brown spots; tibiae with brown spots at bases of spines, which fade apically; tarsi yellowish to pale brown; claws (Fig. 53) brownish.

Male genitalia: Vesica (Fig. 62); phallotheca (Fig. 63); right paramere (Fig. 64); left paramere (Fig. 65).

Remarks. All records of *K. sulphurea* for North America, including most for Florida, should be applied to *K. tuckeri.* Essentially, all workers have followed Knight's (1923) concept of *K. sulphurea,* a species limited in distribution to Jamaica and parts of Florida. *Keltonia sulphurea* has the spots on the hemelytra evenly distributed, whereas *K. tuckeri* (and *K. sulphurea* of Knight and others) has a coalesced cloud of spots through the middle of the corium and apical area of the clavus.

In addition, I note that the material I have associated with *K. tuckeri* from Colombia, El Salvador, Guatemala, Panama, and Venezuela is slightly smaller than

more northern examples of this species, but, otherwise, is inseparable by me at this time based on external characters. However, the spiculum of the male vesica of this southern material tends to be more rounded apically than is typical for specimens of *K. tuckeri*. With the study of more material, this neotropical material may prove to represent a distinct species.

Type material examined. *K. tuckeri* was described from a single specimen taken in Texas. That holotype is in the Mus. Zool., Helsinki with the following labels: 1, "Plano, Texas, Oct. at night, E. S. Tucker"; 2, "Mus. Zool. H:fors Spec. typ. No. 10301, *Pseudatomoscelis tuckeri* Popp."; 3 (red label here added), "Holotype: female, *Pseudatomoscelis tuckeri* Poppius." The condition is fair. Missing are all antennal segments (except both first segments), the right pro- and left metatibiae, and the right middle and right hind legs, and most of the sericeus pubescence is rubbed away.

Other material examined. Colombia—1 ♂, Magdal., Santa Marta, Oct. 8, 1971, G. E. Bohart (USU); 1 ♂, Tol. Armero, June 26–30, 1977, Peyton & Suarez, taken in malaise trap (USNM). **El Salvador**—1 ♂, Tonacatepeque, June 20, 1958, L. J. Bottimer (USNM). **Guatemala**—1 ♂, Yepocapa, Chimatenango, Apr. 7, 1948, H. D. Alberto (USNM). **Honduras**—1 ♂, Coyles, Dec. 20, 1976, G. V. Manley (TAM). **Mexico**—CHIAPAS: 1 ♀, 25 mi SW Cintalapa, July 11, 1971, Clark, Murray, Hart, & Schaffner (TAM); 1 ♀, 3 mi SW Cintalpa, 19 Oct. 1976, Cate & Clark (TAM). GUERRERO: 1 ♀, Iguala, July 8–9, 1971, Clark, Murray, Hart, & Schaffner (TAM). JALISCO: 4 ♂♂, 16 km N Autlan, July 12–14, 1983, at blacklight, Kovarik, Harrison, & Schaffner (TAM). OAXACA: 5 ♂♂, 1 ♀, 9 mi W Tehuantepec, VI-25-65, at light, Burke, Meyer, & Schaffner (TAM); 45 ♂♂, 11 ♀♀, 12 mi W Tehuantepec, July 11, 1971, at light, Clark, Murray, Hart, & Schaffner (TAM, USNM); 3 ♂♂, 2 ♀♀, 6 mi W Tehuantepec, July 6, 1971, at light, Clark, Murray, Hart, & Schaffner (TAM); 14 ♂♂, 8 ♀♀, 11.6 mi W Jalapa de Marques, July 12, 1971, at light, Clark, Murray, Hart, & Schaffner (TAM, USNM); 1 ♂, 11 mi W Tehuantepec, July 23, 1973, Mastro & Schaffner (TAM); 6 ♂♂, 9 mi W Tehuantepec, July 17, 1973, at light, Mastro & Schaffner (TAM); 1 ♂, 12 mi W Zanatepec, July 18, 1973, Mastro & Schaffner (TAM); 6 ♂♂, 5 ♀♀, 2 mi N Totlapan, July 17, 1973, Mastro & Schaffner (TAM); 7 ♂♂, 5 ♀♀, 8 mi N La Vertosa, July 22, 1973, at light, Mastro & Schaffner (TAM); 2 ♂♂, 1 mi SW Rio Hondo, July 22, 1974, Clark, Murray, Ashe, & Schaffner (TAM); 5 ♂♂, 2 ♀♀, 2.7 mi NW El Cameron, July 21–22, 1974, Clark, Murray, Ashe, & Schaffner (TAM); 1 ♂, 10.5 mi W Tehuantepec, July 22, 1974, Clark, Murray, Ashe, & Schaffner (TAM); 8 ♂♂, 2.1 mi NW Totolapan, July 11–17, 1981, Bogar, Schaffner, & Friedlander (TAM). PUEBLA: 1 ♀, 13.3 mi NE Tehuitzingo, July 13–14, 1974, Clark, Murray, Ashe, & Schaffner (TAM). QUERETARO: 1 ♀, 1 mi NW Ayutla, July 24, 1970, at light, Murray, Phelps, Hart, & Schaffner (TAM). **Panama**—2 ♀♀, Pt. Aguadulce, Nov. 21, 1952, F. S. Blanton (USNM); 1 ♀, Rio Sajalises, near Villa Real, Sept. 12, 1952, F. S. Blanton (USNM). **United States**—ALABAMA: [Cullman Co.] Garden City, July 7, 1939, D. E. Hardy (KU); 1 ♀, [Jefferson Co.] Edgewood, Birmingham, Aug. 10, 1916, Ac 4849 (AMNH); 2 ♂♂, 5 ♀♀, [Montgomery Co.] Pickett Springs, Montgomery Aug. 5–6, 1916, Ac. 4849 (AMNH); 1 ♀, [Morgan Co.] Decatur, July 6, 1939, P. B. Lawson (KU); 2 ♂♂, 2 ♀♀, [Tallapoosa Co.] Alexander City, G. Nelson, Aug. (AMNH). ARIZONA: 1 ♂, [Maricopa Co.] Buckeye, 6-12-35, H. G. Johnston, on *Salvia* (USNM); 4 ♂♂, 1 ♀, [Maricopa Co.] Palo Verde, 6-20-1935, H. G. Johnston, on wild sunflower (USNM); 1 ♀, [Pima Co.] San Xavier, Mission, X-15-36, E. P.

Van Duzee (CAS). ARKANSAS: 6 ♂♂, 12 ♀♀, Newton Co., Rt. 74, nr. Jasper, June 16, 1987, T. J. Henry & A. G. Wheeler, Jr., taken on *Aster* sp., poss. *pilosus* (USNM); 2 ♂♂, 3 ♀♀, Polk Co., 7-21-28, L. D. Beamer (KU); 1 ♀, Washington Co., VI-30-1940, M. W. Sanderson (KU). COLORADO: 21 ♂♂, 23 ♀♀, Douglas Co. Waterton, June 18–30, 1981, J. T. Polhemus, taken on *Chrysopsis villosa* (JTP); 2 ♂♂, 2 ♀♀, [Douglas Co.] Perry Park, CL873, July 13, 1977, D. A. & J. T. Polhemus (JTP); 1 ♀, Jefferson Co., O'Fallen Park, nr. Kittridge, Aug. 31, 1981, D. A. Polhemus (JTP); 11 ♂♂, 15 ♀♀, Mesa Co., John Brown Creek, 5 mi W of Gateway, 15 Aug. 1987, T. J. Henry, D. A. & J. T. Polhemus, taken on *Chrysopsis villosa* (USNM). DISTRICT OF COLUMBIA: 1 ♀, July 3, 1926, H. H. Knight (USNM): 1 ♂, 1 ♀, Nat'l. Arboretum, 27 Sept. 1981, T. J. Henry & A. G. Wheeler, Jr., on *Ambrosia artemisiifolia* (USNM). FLORIDA: 1 ♂, [Alachua Co.] Waldo, 8-18-1930, L. D. Tuthill (KU); 2 ♀♀, [Alachua Co.], Waldo, 4 May 1961, L. A. Kelton (CNC); 1 ♂, 2 ♂♂, Gilchrist Co., Trenton, 2 May 1981, T. J. Henry, on *Eupatorium capillifolium* (USNM); 2 ♀♀, Marion Co., Rt. 40, 2 mi E Lynne, 24 Apr. 1984, T. J. Henry & A. G. Wheeler, Jr., on *Heterotheca* sp.; 1 ♀, [Nassau Co.] Hilliard, 8-19-1930, J. Nottingham (KU); 3 ♂♂, 1 ♀, Okaloosa Co., 5 mi N Crestview, 11 May 1982, T. J. Henry, on *Gaillardia pulchella* (USNM); 1 ♂, 1 ♀, [Putnam Co.] Crescent City, Apr. 1908, Van Duzee (CAS); 1 ♂, [Suwanee Co.] Branford, 7-31, 1930, R. H. Beamer (KU); 1 ♂, Taylor Co., Salem, VIII-29-1960, L. A. Stange (UCD); 1 ♀, [Leon Co.] Tallahassee, 7-14-1934, P. A. McKinstry (KU); 2 ♂♂, [Seminole Co.] Sanford, 8-22-1933, C. O. Bare (KU). GEORGIA: 3 ♂♂, 2 ♀♀, Clarke Co., Stonehenge, 8–14 May 1974, C. L. Smith, at light (USNM); 1 ♀, Clarke Co., 7 mi SW Winterville, 19 May 1974, C. L. Smith, at light (USNM); 1 ♂, Oconee Co., Decalb Farm, 22 July 1971, C. L. Smith, light trap (USNM). ILLINOIS: 1 ♂, [Alexander Co.] Olive Branch, 9-24-1941, R. L. McCarr, on cotton (USNM); 1 ♂, [Wayne Co.] Fairfield, June 12, 1934, DeLong & Ross (ANMH); 1 ♂, [county?] Meredosia, Aug. 22, 1898, F. M. McE. (AMNH). KANSAS: 2 ♂♂, [Douglas Co.] Lawrence, 9-20-1944, R. H. Beamer (KU). LOUISIANA: 2 ♂♂, [county?] Opelousas, G. R. Pilate, no collector or date (USNM). MARYLAND: 1 ♂, 1 ♀, Prince Georges Co., Hyattsville, Sept. 6, 1914, W. L. McAtee, on *Solanum* "*carolinianum*" (USNM); 2 ♂♂, Prince Georges Co., Lanham, 6-25, 1967, P. Oman (OSU). MASSACHUSETTS: 1 ♂, [Dukes Co.] Edgartown, 22 Aug. 1912, Parshley colln. (CNC). MISSISSIPPI: 1 ♂, 5 ♀♀, [Itawamba Co.] Fulton, 7-14-1930, P. W. Oman (KU); 1 ♂, [Lauderdale Co.] Meridian, 7-17-1930, L. D. Tuthill (KU); 1 ♀, [Leake Co.] Carthage, 25 Aug. 1928, H. G. Johnston [TAM); 1 ♂, 4 ♀♀, [Lowndus Co.] Columbus, 7-16-1930, R. H. Beamer (KU); 1 ♂, [Monroe Co.] Hamilton, 7-15-1930, P. W. Oman (KU); 1 ♂, [Noxubee Co.] Shuqualak, 7-16, 1030, R. H. Beamer (KU). MISSOURI: 3 ♂♂, 2 ♀♀, [Taney Co.] Hollister, July 22, 1915, H. H. Knight (USNM). NEW JERSEY: 1 ♂, [Cape May Co.] Woodbine, 8-21-1902, E. P. Van Duzee (CAS). NORTH CAROLINA: 1 ♂, 1 ♀, Brunswick Co., Shallotte Point, 11 July 1960, P. D. Ashlock (CNC); 1 ♂, 12 ♀♀, Guilford Co., Greensboro, 17 June 1956, P. D. Ashlock (CNC); 1 ♂, [Macon Co.] Whiteface Cove, nr. Highlands, 17 Aug. 1957, L. A. Kelton, ex. ragweed (CNC); 1 ♂, [Macon Co.] Highlands, Horse Cove, 9 Aug. 1957, L. A. Kelton (CNC); 1 ♂, 1 ♀, [Johnson Co.] Benson, 8-9-1934, R. H. Beamer (KU); 1 ♂, [Shelby Co.] Raleigh, 8-30-1946, R. H. Beamer (KU); 1 ♀, Wake Co., 13 June 1958, D. A. Young (CNC). PENNSYLVANIA: 1 ♂, Dauphin Co., Conewago Twp., Cedar Rd., 28 June 1977, T. J. Henry, taken at light (USNM). SOUTH CAROLINA: 1 ♂, 2 ♀♀, [Aiken Co.]

Aiken, 24 Aug. 1957, W. R. Richards (CNC); 1 ♂, [Lexington Co.] Batesburg, 8-21-1930, J. Nottingham (KU); 3 ♂♂, 2 ♀♀, [Oconee Co.] Seneca, 20 Aug. 1957, W. R. Richards & L. A. Kelton (CNC). TENNESSEE: 5 ♂♂, 1 ♀, Hamilton Co., 6-24-1943, Turner 20294, light trap at edge of peach orchard (USNM). TEXAS: 1 ♂, 1 ♀, Anderson Co., Salmon, 14–21 July 1974, H. R. Burke, taken from malaise trap (TAM); 1 ♂, Bell Co., Temple, Weems Farm, 31 01′ L 97 12′, 23 Sept. 1986, W. A. Palmer, taken on *Amaranthus psilostachys* (TAM); 1 ♂, 4 ♀♀, Bosque Co., 2 mi W Iredell, 22 May 1970, J. C. Schaffner (TAM); 1 ♂, 1 ♀, Brazoria Co., 6 Aug. 1968, D. P. Sanders (TAM); 15 ♂♂, 13 ♀♀, Brazos Co., Bryan, 28 Apr.–11 Oct. 1965–1975, J. C. Schaffner, at light (TAM); 3 ♂♂, 1 ♀, Brazos Co., College Stn., 12 Oct. 1928, S. E. Jones, at light (TAM); Brazos Co., College Stn., 28 May 1928, taken on *Amaranthus torreyii* and *Heterotheca subaxilaris* (TAM); 2 ♂♂, Brazos Co., College Stn., 10 May 1928, H. G. Johnston (TAM); Brazos Co., College Stn., 1 May 1973, W. E. Clark (TAM); 2 ♂♂, Brazos Co., College Stn., 6 May 1975, J. C. Schaffner, at light (TAM); 1 ♂, 1 ♀, Brazos Co., Koppe's Bridge, 5 mi SW Welborn, 22 June 1972, E. E. Grissell (TAM); 2 ♂♂, Brazos Co., Jones Rd., 1.6 mi N Hwy. 60, 1 June 1975, S. J. Merritt (TAM); 1 ♀, Brazos Co., Cedar Creek, 5 Sept. 1970, Board & Phelps, at light (TAM); 1 ♀, Burnet Co., Inks Lake St. Pk., 18 June 1965, M. H. Sweet (TAM); 1 ♀, Hidalgo Co., Bentsen-Rio Grande St. Pk., 18 June 1969, Board & Hafernik (TAM); 1 ♀, Hill Co., 15 mi W West, 26 Aug. 1971, J. C. Schaffner (TAM); 1 ♂, Robertson Co., 2.9 mi N Jct. OSR and FM 46, 24 July 1976, S. J. Merritt, sweeping *Monarda* (TAM); 5 ♂♂, 6 ♀♀, Kleburg Co., N Padre Island, 21 Apr. 1983, T. J. Henry & A. G. Wheeler, Jr., on *Heterotheca subaxilaris* (USNM); 2 ♂♂, 3 ♀♀, Kleburg Co., Nueces Bay, Corpus Christi, 19 Apr. 1983, T. J. Henry & A. G. Wheeler, Jr., on *Heterotheca subaxilaris* (USNM); 1 ♀, San Patricio Co., Lake Corpus Christi St. Pk., 8 June 1969, Board & Hafernik (TAM); 1 ♂, 1 ♀, San Patricio Co., Welder Wildlife Refuge, 25 June 1981, J. C. Schaffner (TAM); 1 ♂, Washington Co., Lake Somerville, 18 Apr. 1971, J. C. Schaffner (TAM). UTAH: 2 ♂♂, [Washington Co.] Zion Nat'l. Park, V. M. Tanner (USNM). VIRGINIA: 1 ♀, [Albemarle Co.] Charlottesville, 8-30-1930, L. C. Woodruff (KU). **Venezuela**—3 ♂♂, 3 ♀♀, Zulia, 6 km W La Concepcion, June 18, 1976, A. S. Menke & D. Vincent (USNM); 4 ♂♂, 1 ♀, Lara, 12 km N Cubrio, 800 m, Acacia & secondary growth, Dec. 27, 1985, P. Kovarik & R. Jones (TAM); 2 ♂♂, 4 ♀♀, Lara, 6 km S El Tocuyo, Acacia savannah, 700 m, Dec. 29, 1985, P. Kovarik & R. Jones (TAM).

Distribution. All distribution records for *K. sulphurea,* except Jamaica, as given by Henry and Wheeler (1988), should be applied to *K. tuckeri.* This species occurs across the United States from Massachusetts west to Colorado, and south through Mexico and Central America to Colombia and Venezuela. It is recorded from Alabama, Arizona, Arkansas, Connecticut, Delaware, District of Columbia, Florida, Georgia, Illinois, Kansas, Massachusetts, Mississippi, Missouri, North Carolina, Ohio, Texas, West Virginia, and Mexico. New United States records are Colorado, Louisiana, New Jersey, Pennsylvania, South Carolina, Tennessee, Utah, and Virginia. New country records are Colombia, El Salvador, Guatemala, Honduras, Panama, and Venezuela.

Hosts. *Keltonia tuckeri* (as *K. sulphurea*) has been recorded from *Ambrosia artemisiifolia* L. [Asteraceae], *A. trifida* L., *Aster pilosus* Willd. [Asteraceae], *Chenopodium album* L. [Chenopodiaceae], *Conyza canadensis* L. [Asteraceae], *Eupatorium serotinum* Michx. [Asteraceae], *Haplopappus divaricatus* (Nutt.) Gray [Asteraceae], *He-*

lenium amarum (Raf.) H. Rock [Asteraceae], *Heterotheca latifolia* Buckl. [Asteraceae], *Iva annua* L. [Asteraceae], *Oenothera laciniata* Hill. [Onagraceae], *Sida spinosa* L. [Malvaceae], *Solanum carolinense* L. [Solanaceae], *Symphorocarpos orbiculatus* Moench [Caprifoliaceae], and *Xanthium strumarium* L. [Asteraceae] (Knight, 1927, 1941, 1966; Knight and McAtee, 1929; Snodgrass et al., 1984). New records based on specimens studied include: *Amaranthus* "*psilostachys*" [Amaranthaceae], *A. torreyii* Benth., *Chrysopsis villosa* DC. [Asteraceae], *Eupatorium capillifolium* (Lam.) Small [Asteraceae], *Gaillardia pulchella* Foug. [Asteraceae], *Heterotheca subaxilaris* (L.) Britt. & Rusby [Asteraceae], *Monarda* sp. [Lamiaceae], and *Salvia* sp. [Lamiaceae].

In the eastern U.S., I have collected adults and nymphs of this species most frequently on *Ambrosia* spp.; in Colorado it was abundant on *Chrysopsis villosa*; and in Texas it was common on *Heterotheca subaxilaris*. Based on the numerous hosts listed above, especially those having immatures associated with them, *K. tuckeri* would appear to be primarily a composite (Asteraceae) specialist.

McPherson et al. (1983) studied the flight patterns of this species (as *K. sulphurea*) in North Carolina, noting that 85% of the adults were captured in their traps at a height of 1 meter. They also speculated that this species, which overwinters in the egg stage, probably has 3 generations (in N.C.), based on peak flight activity from late May to mid-July, mid-July to late August, and early September to October.

Pseudatomoscelis Poppius

Pseudatomoscelis Poppius, 1911:85; Carvalho, 1959: Addenda et Corrigenda (as synonym of *Psallus* Fieber); Knight, 1968:55; Sterling and Dean, 1977:1–28; Kelton, 1980:330; Henry and Wheeler, 1988:495. Type species: *Atomoscelis seriatus* Reuter, 1876. Original designation.

Diagnosis. Phylinae: Phylini. This genus is distinguished from all other genera in the tribe Phylini by the pale (pale green or yellow to pale orange) to green body coloration; 3 or more distinct fuscous spots or bands on the 2nd antennal segment, pale to brownish membrane with a dark fuscous mark just posterior to apex of the cuneus; one or more dark setal patches along inner margin of cuneus (and paracuneus) bordering membrane; two types of pubescence, with sericeus setae present in distinct clumps (but not in rows along midline as in *Keltonia*); dark bristlelike setae on dorsal edge of metafemur, pale tibiae with dark spots at the bases of the spines; the stoutly formed, C-shaped vesica, with a slender acuminate spiculum (lacking the apical, bluntly rounded, shallow cuplike process found in species of *Keltonia*); and the phallotheca with a subapical spine.

Description. Generally elongate oval, delicate, small sized, length from apex of tylus to apex of hemelytral membrane 2.15–3.40 mm; coloration pale yellow to dark green, or yellowish orange; dorsum impunctate, surface shiny to almost velvety, clothed with simple, often bristlelike, semierect setae, intermixed with individual or tufts (clumps of 2–6 setae) of silvery, sericeus or scalelike setae. Head subtriangular in dorsal aspect, tylus somewhat thickened, rounded apically; antennal segment I not or just surpassing apex of tylus, antennal fossa or socket set anteriorly adjacent to lower edge of compound eye just below emargination (Fig. 67), eyes sparsely pubescent; tufts of sericeus setae present at base of jugum and along inner margin of eye

near antennal fossa (Fig. 68), individual setae scattered over frons and vertex. Rostrum extending just beyond metacoxae to 2nd or 3rd abdominal segment. Antenna slender, segment I shortest and thickest, apex only slightly surpassing apex of tylus, II longest, nearly as thick as segment I in males, always possessing 3 or more dark spots or bands, III and IV most slender. Pronotum trapeziform, immaculate or spotted, with scattered simple and sericeus setae. Hemelytron macropterous, surface immaculate to uniformly spotted, spots when present fine and dark; cuneus longer than wide at base, inner margin bordering membrane with one or two (counting paracuneus) darkly pigmented patches giving rise to stout fuscous to black setae; membrane pale translucent brown to whitish, with a relatively large fuscous spot near apex of cuneus. Legs slender; femora somewhat thickened, weakly saltatorial, with fine to large dark spots, dorsal edge of metafemora with 6 stout, black, bristlelike setae; tibiae pale with fuscous spots at bases of spines; claws slender, with setiform parempodia and fleshy, quadrate pulvilli (Fig. 70). Male genitalia: Left paramere typically phyline with two parallel processes, the anterior (right) process long and slender, the posterior (left) short and blunt; right paramere flattened, elongate oval, with a short pointed process apically; vesica stout, weakly twisted, C-shaped, lacking shallow, cuplike process [found in *Keltonia*] apically.

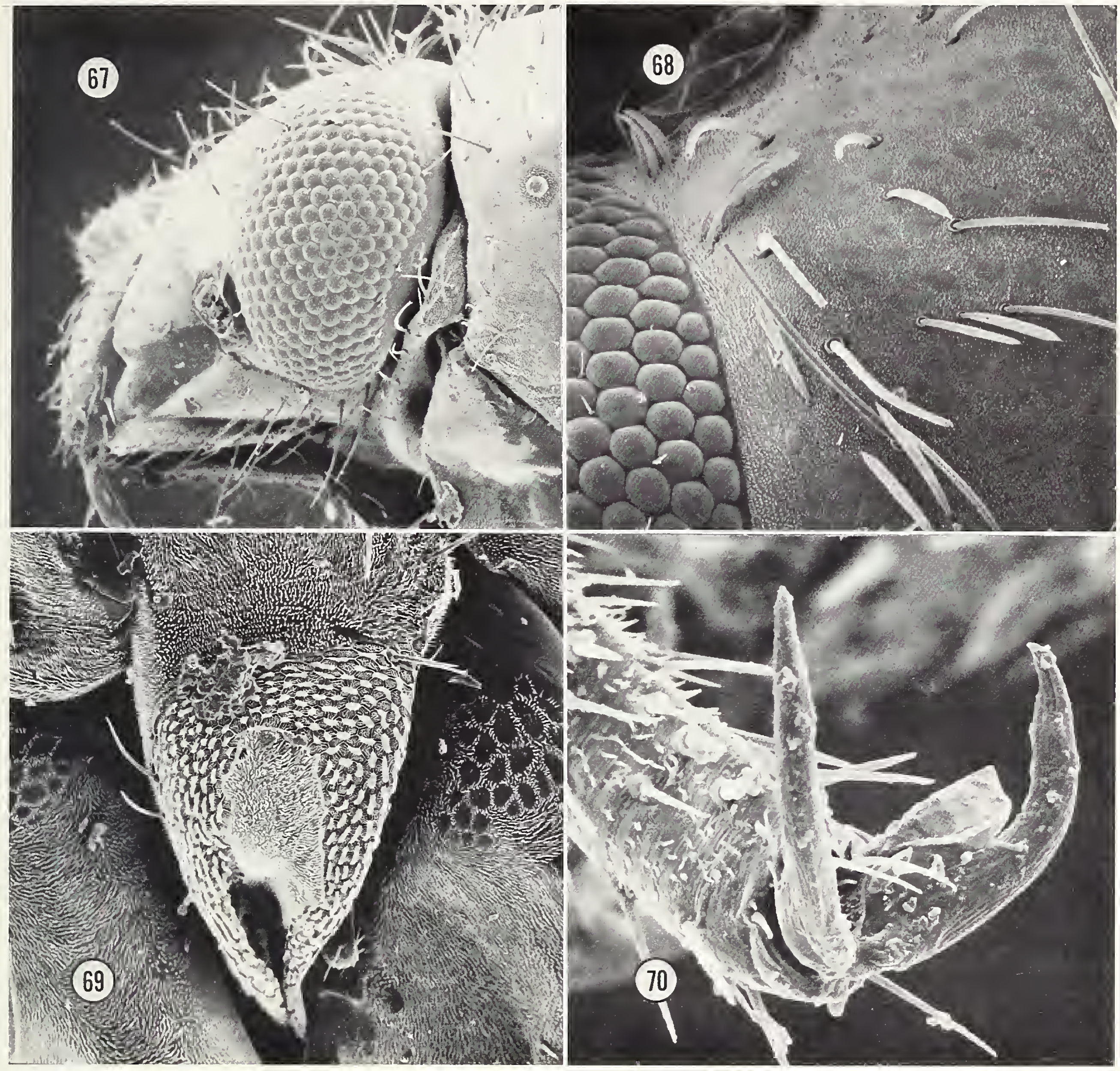
Females are similar to males in color and pubescence, but usually differ by their larger and broader body form, proportionately smaller eyes, broader vertex, and more slender 2nd antennal segment.

Remarks. This genus is mostly closely related to *Keltonia* based on the shared setigerous black spots on the inner margin of the cuneus and paracuneus, two types of pubescence, including the unique tufts of silvery sericeus setae, the spots at the bases of the tibial spines, the large dark spot on the membrane near the apex of the cuneus, and the stout, C-shaped vesica. However, all three species of *Pseudatomoscelis* can be separated from those in *Keltonia* by the spotted 2nd antennal segment, the nonconspurcate hemelytral membrane, and the vesica that lacks an apical process.

Schuh (1984) noted a superficial resemblance of *Pseudatomoscelis seriatus* to the Indo-Pacific phyline *Opuna annulatus* (Knight), presumably based on the similar coloration and spots on the antennae and legs. I have studied a series of *O. annulatus* (females) from Guam, Malaysia, Okinawa, and Thailand and I have compared Schuh's (1984) figures of male genitalia, and concur that the resemblance appears only superficial. The male vesica of *O. annulatus* is sigmoid or S-shaped and lacks the apical sheathlike area found in species of *Pseudatomoscelis,* the appendages of the left paramere are much stouter, and the body lacks sericeus pubescence. I do note that *O. annulatus* possesses dark setal patches along the inner margin of the cuneus, a character I consider synapomorphic for *Keltonia* and *Pseudatomoscelis.* However, because of the lack of other corroborative characters, these patches, along with the spotted 2nd antennal segment, probably are examples of convergence. Only a broader analysis of the phyline genera on a world basis will resolve relationships of such problematic taxa.

KEY TO SPECIES OF *PSEUDATOMOSCELIS*

1. Dorsum immaculate, without spots; body coloration yellow to yellowish orange (Fig. 44); Arizona and Mexico .... *flora* (Van Duzee)



Figs. 67–70. SEM micrographs of *Pseudatomoscelis seriatus*: 67. Lateral aspect of head (145×). 68. Sericeus setae along inner margin of eye (350×). 69. Ostiolar opening and evaporative area. 70. Pretarsal structure (303×). 70. Pretarsal structure (841×).

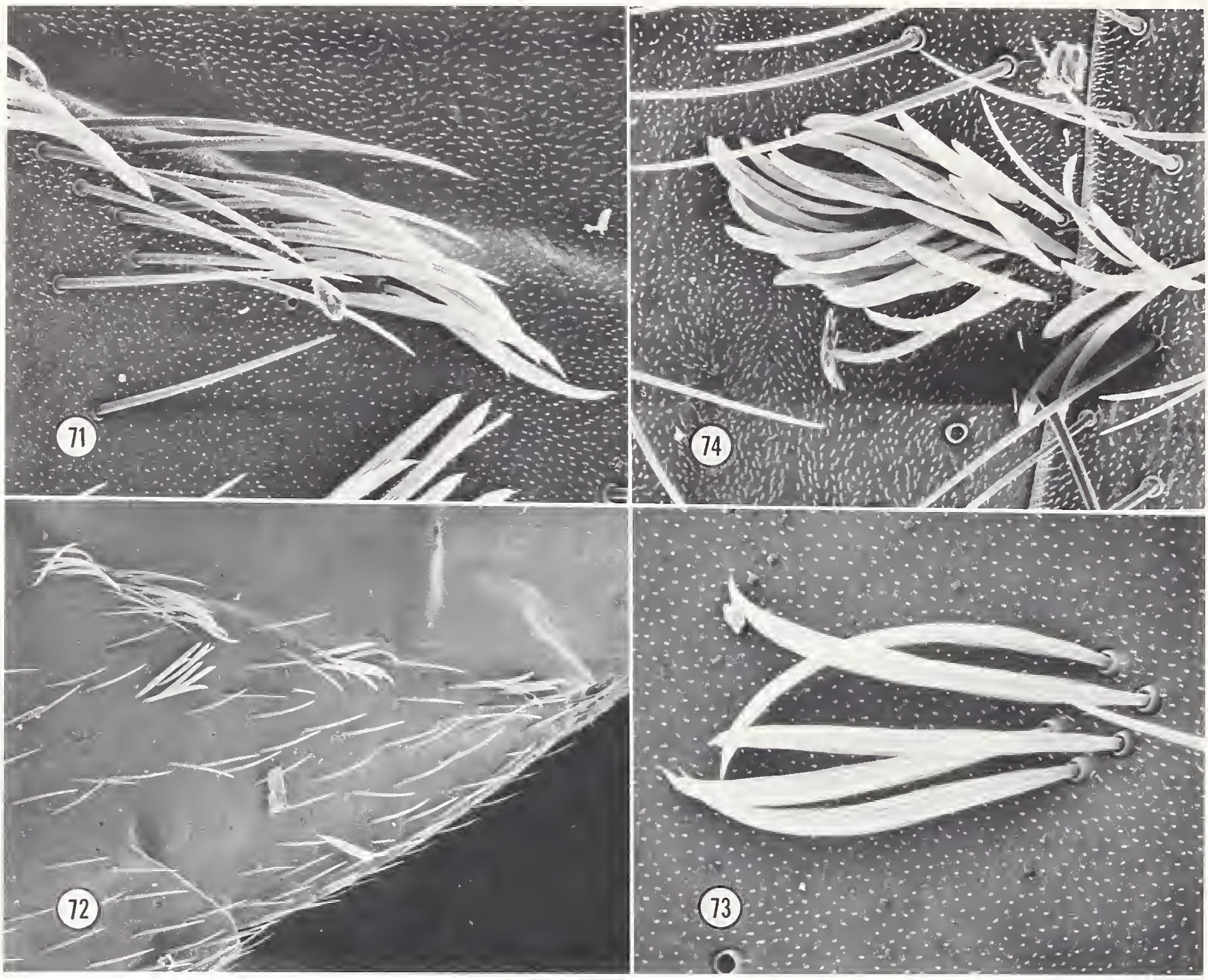
– Dorsum always with dark spots; body coloration pale yellow to dark green, sometimes tinged with yellowish orange 2

2. Small species, length 2.60 mm or less; inner margin of cuneus without or with only vague spots bearing 2 or 3 bristlelike setae; vesica of male (Fig. 79) short and stout; Puerto Rico and St. Thomas, West Indies .... **insularis**, n. sp.

– Larger species, length 2.75 mm or more; inner margin of cuneus with 1 or 2 distinct dark spots bearing numerous dark bristlelike setae; vesica of male (Fig. 83) more slender; Saskatchewan, Canada south to Venezuela, and the West Indies .... *seriatus* (Reuter)

Pseudatomoscelis flora (Van Duzee), **New Combination**
Figs. 44, 75–78

Psallus flora Van Duzee, 1923:158; Carvalho, 1958:121; Bibby, 1961:329; Henry and Wheeler, 1988:493.



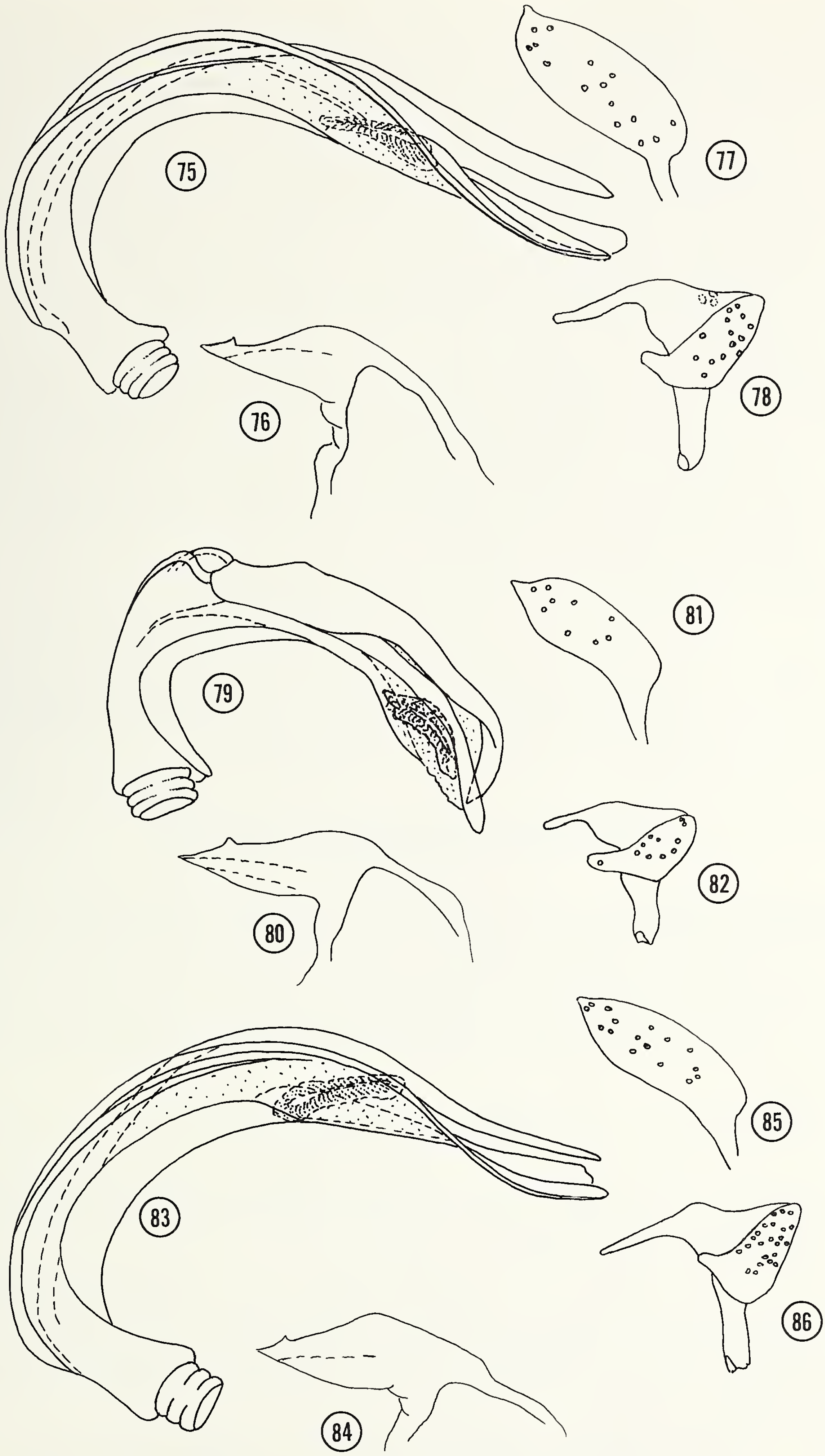
Figs. 71–74. SEM micrographs of setal types. *Pseudatomoscelis seriatus*: 71. Patch of bristlelike and sericeus setae along inner margin of cuneus (901×). 72. Patches of setae along inner margin of cuneus (149×). 73. Cluster of sericeus setae on corium (584×). *Keltonia tuckeri*: 74. Sericeus setae on corium (470×).

Diagnosis. This species is readily distinguished from *P. insularis* and *P. seriatus* by the deep-yellow to yellowish-orange coloration and lack of spots on the dorsum.

Description. Male (N = 5): Length 2.42–3.33 mm, width 1.20–1.32 mm. *Head:* Width 0.70–0.78 mm, vertex 0.34–0.40 mm. *Rostrum:* Length 0.76–0.90 mm, extending to bases of mesocoxae. *Antenna:* Segment I, length 0.20–0.22 mm; II, 0.70–0.78 mm; III, 0.44–0.50; IV, 0.30–0.32 mm. *Pronotum:* Length 0.50–0.62 mm, basal width 1.10–1.20 mm.

Female (N = 4): Length 3.12–3.40 mm, width 1.44–1.48 mm. *Head:* Width 0.72–0.74 mm, vertex 0.36–0.40 mm. *Rostrum:* 0.98–1.00 mm, extending to mesocoxae. *Antenna:* Segment I, length 0.22–0.24 mm; II, 0.82–0.90 mm; III, 0.46–0.50 mm; IV, 0.26–0.34 mm. *Pronotum:* Length 0.62–0.64 mm, basal width 1.18–1.20 mm.

Coloration uniform deep yellow to yellowish orange; dorsum clothed with pale to brown, semierect, simple pubescence, intermixed with individual and small tufts (2–4 setae) of silvery, sericeus setae. Head yellow, with a tuft of sericeus setae at base of buccula and 2 to 3 tufts along inner margin of eye. Antenna pale yellow; segment I with 1 or 2 dark spots on inner apical surface, each spot giving rise to a dark,



Figs. 75–86. Male genitalia of *Pseudatomoscelis* spp. *P. flora*: 75. Vesica. 76. Phallotheca. 77. Right paramere. 78. Left paramere. *K. insularis*: 79–82. *K. seriatus*: 83–86.

bristlelike seta; II pale yellow, with 3 to 4 evenly spaced dark-brown spots; III yellow, with a narrow, dark-brown band at base; IV yellow. Pronotum uniformly yellow, with scattered simple and sericeus setae. Scutellum and hemelytron uniformly yellow, with scattered simple and individual and tufts of sericeus setae; cuneus yellow, with inner basal angle (paracuneus) bearing a dark spot giving rise to a cluster of fuscous or black bristlelike setae; membrane translucent white with a brown apical cloud and a dark spot posterior to apex of cuneus; veins yellow. Ventral surface yellow. Legs yellow; femora finely brown spotted on apical halves; tibiae yellow with brown spots at bases of fuscous tibial spines; tarsi yellow; claws brown.

Male genitalia: Vesica (Fig. 75); phallotheca (Fig. 76); right paramere (Fig. 77); left paramere (Fig. 78).

Specimens examined. Mexico—BAJA CALIFORNIA SUR: 1 ♂, 1 ♀ (paratypes), Mulegé, 14 May 1921, E. P. Van Duzee [taken on *Wislizenia refracta*] (USNM); 1 ♀, intercepted at El Paso, Texas from Mexico, x-19-48, with mustard (USNM). **United States**—ARIZONA: 3 ♂♂, 4 ♀♀, Pima Co., 29 Sept. 1940, L. L. Stitt, taken on *Wislizenia refracta* (USNM); 5 ♂♂, 5 ♀♀, Pima Co., No. 1505, 4 May 1958 [F. F. Bibby], taken on *Wislizenia refracta* (USNM).

Distribution. Known only from Arizona and Baja, Mexico.

Hosts.—Van Duzee (1923), in the original description, wrote "on the yellow flowers of *Wislizenia refracta* [Engelm., Capparidaceae], the color of which they match exactly." Bibby (1961), in reporting the first U.S. record, also listed *W. refracta* as the host. The record "with mustard" on a specimen in the USNM collection probably represents a sitting record or a plant misidentification.

Pseudatomoscelis insularis, new species
Figs. 79–82

Diagnosis. This species is distinguished from *P. flora* by the presence of distinct spots on the dorsum. From *P. seriatus,* it is recognized by the small size (males 2.40 mm or less; females 2.60 mm or less), and shorter, stouter, more curved, male vesica. Also, the head, and often the pronotum, of *P. insularis* is much less profusely spotted than on *P. seriatus,* and the dark patches on the inner margin of the cuneus are much less distinct.

Description. Male (N = 6): Length 2.16–2.40 mm, width 1.10–1.12 mm. *Head:* Width 0.60–0.62 mm, vertex 0.28–0.30 mm. *Rostrum:* Length 1.10–1.12 mm, extending to base of genital segment. *Antenna:* Segment I, length 0.20–0.22 mm; II, 0.78–0.80 mm; III, 0.36–0.38 mm; IV, 0.24–0.26 mm. *Pronotum:* Length 0.44–0.46 mm, basal width 0.88–0.90 mm.

Female (N = 6): Length 2.40–2.60 mm, width 1.10–1.18 mm. *Head:* Width 0.58–0.60 mm, vertex 0.30–0.32 mm. *Rostrum:* Length 1.08–1.16 mm, extending to base of ovipositor. *Antenna:* Segment I, length 0.20–0.22 mm; II, 0.76–0.78 mm; III, 0.36–0.38 mm; IV, 0.24–0.28 mm. *Pronotum:* Length 0.44–0.46 mm, basal width 0.86–0.96 mm.

General coloration pallid to greenish yellow, with pronotum, scutellum, and hemelytra uniformly sprinkled with small brown spots, each spot giving rise to an erect to semierect, fuscous, bristlelike seta, intermixed with tufts of silvery sericeus setae. Head pallid to greenish yellow, often strongly tinged with deeper orange yellow,

sometimes with a few scattered brown spots, especially along base of vertex and across anterior edge of frons; set with long, erect, dark, bristlelike setae, intermixed with tufts of silvery sericeus setae on tylus, lorum, vertex, and 2 patches along inner margin of eye. Antenna pallid; segment I with a subapical and subbasal fuscous band, usually darkest on inner surface; segment II with 3–5 dark spots, most distinct dorsally; segment III brown, with a fuscous band at base; segment IV dark brown. Pronotum greenish yellow, tinged with orange yellow on calli, spots varying from uniformly sprinkled, except on area of calli, to nearly absent, each spot giving rise to a dark bristle. Hemelytron pallid to greenish yellow, often strongly tinged with deep orange yellow; uniformly spotted, with widely scattered tufts of 3–6 silvery sericeus setae; inner margin cuneus with 2 dark patches of dark bristlelike setae; membrane dark smoky brown, with a large darker spot just beyond apex of cuneus, area adjacent to apex of cuneus and posterior to dark spot pallid; veins pallid to orange yellow. Ventral surface greenish yellow, usually with a streak of orange or orange yellow on propleura, mesopleura, and prosternum; abdomen greenish yellow, with scattered brown spots, sides usually tinged with orange yellow. Legs pallid; femora thickly brown spotted, metafemora with 6 dorsal, stout, bristlelike setae; tibiae with large dark spots at bases of stout black spines; tarsi pale, becoming darker apically; claws fuscous.

Male genitalia: Vesica (Fig. 79); phallotheca (Fig. 80); right paramere (Fig. 81); left paramere (Fig. 82).

Type specimens. Holotype ♂: Puerto Rico, Puente Blanco Quebradillas, 10 June 1990, A. G. Wheeler, Jr., beaten from *Croton* sp. (USNM). Paratypes: 5 ♂♂, 4 ♀♀, same data as for holotype (USNM); 3 ♀♀, Puerto Rico, Guánica Forest Reserve, 9 June 1990, A. G. Wheeler, Jr., on shrubs (USNM); 3 ♂♂, 6 ♀♀, St. Thomas, Vir. Ids., no specific locality, June 5, 1917, H. Morrison (USNM); 1 ♂, Charlotte Amalie, St. Thomas, Vir. Ids., June 2, 1917, H. Morrison (USNM).

Etymology. This species is named *insularis* after the Latin noun *insula,* meaning island, and refers to its distribution on the islands of Puerto Rico and St. Thomas.

Distribution. Known only from Puerto Rico and St. Thomas.

Hosts. Part of the type series from Puerto Rico was taken on *Croton* sp. (Euphorbiaceae), a common host for *P. seriatus,* as well.

Pseudatomoscelis seriatus (Reuter)
Figs. 66–73, 83–86

Atomoscelis seriatus Reuter, 1876:91; Van Duzee, 1909:183; Van Duzee, 1914:29.
Psallus delicatus: Howard, 1898:101 (misidentification).
Psallus atomophorus Reuter, 1907:22; Van Duzee, 1907:27; Van Duzee, 1909:183. **NEW SYNONYMY.**
Pseudatomoscelis seriatus: Poppius, 1911:86; Knight, 1968:55; Sterling and Dean, 1977:1–28 (bibliography); Kelton, 1980:331 (habitus, p. 286); Snodgrass et al., 1984:851; Schuh and Schwartz, 1985:434, fig. 54; Henry and Wheeler, 1988:495.
Psallus seriatus: Van Duzee, 1916:46; Van Duzee, 1917:407; Blatchley, 1926:957; Knight, 1926a:106, 1926b:36, 1941:45; Carvalho, 1958:131.

Diagnosis. *P. seriatus* is easily distinguished from *P. flora* by the dark-spotted pale to green dorsum. From *P. insularis,* it is separated by the larger size, more profusely

spotted dorsum, especially on head and pronotum, the larger, more distinct cuneal patches, and the longer, more slender vesica.

Description. Male (N = 10): Length 2.76–3.16 mm, width 1.20–1.28 mm. *Head:* Width 0.66–0.70 mm, vertex 0.32–0.36 mm. *Rostrum:* Length 1.32–1.45 mm, extending genital segment. *Antenna:* Segment I, length 0.20–0.22 mm; II, 0.74–0.76 mm; III, 0.46–0.48 mm; IV, 0.30–0.32 mm. *Pronotum:* Length 0.50–0.60 mm, basal width 1.02–1.06 mm.

Female (N = 10): Length 2.80–3.40 mm, width 1.28–1.40 mm. *Head:* Width 0.64–0.72 mm, vertex 0.34–0.38 mm. *Rostrum:* Length 1.30–1.58 mm, extending to base of ovipositor. *Antenna:* Segment I, length 0.22–0.24 mm; II, 0.70–0.86 mm; III, 0.46–0.50 mm; IV, 0.34–0.36 mm. *Pronotum:* Length 0.46–0.60 mm, basal width 1.00–1.16 mm.

General coloration pallid to olive green, with head, pronotum, scutellum, and hemelytra uniformly sprinkled with small to relatively large dark spots, density of spots varying from widely spaced to nearly contiguous, separated only by a distance equal to their own diameter, each spot giving rise to an erect or semierect, fuscous, bristlelike seta, intermixed with tufts of silvery sericeus setae. Head (Figs. 67, 68) colored as remainder of dorsum, often tinged with orange along base of vertex, set with long erect and semierect yellowish-brown setae, intermixed with 2 tufts of sericeus setae along inner margin of each eye and scattered tufts on frons, vertex, and around base of tylus. Antenna pale; segment I with a dark subapical spot, and on darker specimens often with a dark spot at base; segment II with 3–6 dark spots, on dark specimens spots almost forming bands; segment III pale to dusky, with a narrow dark band at base; segment IV dusky. Pronotum colored as remainder of dorsum, often tinged with orange on calli, set with simple yellowish-brown, dark bristlelike, and scattered silvery sericeus setae. Hemelytron, including cuneus, uniformly spotted, with scattered tufts of 3–6 silvery sericeus setae (Fig. 73); inner margin of cuneus (Figs. 71, 72) with 2 dark patches formed by clusters of stout, dark, bristlelike setae. Membrane translucent smoky brown, with a dark to fuscous triangular spot near apex of cuneus and a large, quadrate transparent area just beyond; veins pale. Ventral surface pale green to darker olive green, abdomen usually with small scattered spots; pro- and mesopleura each often with a pale orange spot or streak; ostiole (Fig. 69). Legs pale or pale green; femora thickly spotted, metafemur with dorsal edge of metafemur with a row of stout, erect, black, bristlelike setae; tibiae pale with large dark spots at bases of stout black spines; tarsi pale yellowish brown; claws (Fig. 70) fuscous.

Male genitalia: Vesica (Fig. 83); phallotheca (Fig. 84); right paramere (Fig. 85); left paramere (Fig. 86).

Remarks. *Pseudatomoscelis seriatus* is highly variable in coloration, density of the dorsal spots, and size, all of which appear to be greatly influenced by host plants. Specimens in the southern United States from *Croton* spp. and cotton are pale with rather sparse, small, dorsal spots. Specimens taken in Florida on *Syngonathus flavidulus* (Michx.) Rhuland are smaller, much darker (olive green), and the dorsal spots are larger and more dense, differing to the extent of suggesting a separate species. However, based on relative measurements and male genitalia, all of these individuals appear conspecific.

Type designations. I have studied a male in the California Academy of Sciences

that apparently is the only specimen remaining of the original type series of *P. atomophorus*. It is in very poor condition, having the head and all legs and antennae missing, and the pronotum is separated from but still attached to the body. The vesica allows me to conclude the species is conspecific with *P. seriatus*. It is interesting that Van Duzee (1909), in discussing *P. seriatus,* noted that "This species has much the aspect of *Psallus atomophorus* Reuter from Jamaica." For nomenclatural stability this specimen is here designated the lectotype with the following labels: label 1, "Kingston, Ja., Apr. 06"; 2, "VanDuzee Collector"; 3, "EPVanDuzee Collection"; 4 (handwritten), "Psallus atomophorus Reut., Comp. w. type"; 5 (here added), "Lectotype: ♂, Psallus atomophorus Reuter by T. J. Henry."

I have not studied any type material of *Atomoscelis seriatus* described from "Texas (Belfrage)." However, *P. seriatus* is the only pale North American mirid that possesses dorsal spots and spotted antennae and, thus, I have no doubt about the identity of Reuter's species.

Other specimens examined. Because *P. seriatus* is well known in the United States and I have discovered only one new state record from the several thousand specimens studied, only data for material taken outside the U.S., except the new Nevada record, are given (see U.S. distribution and hosts listed below). **Dominican Republic**—2 ♀♀, Barahora Prov., 13 VII 1967, L. H. Rolston (TAM). **Honduras**—2 ♂♂, Puerto Costilla, 2 IV 1926, R. H. Painter (TAM). **Jamaica**—1 ♂ (lectotype of *P. atomophorus*), Kingston, Apr. 1906, Van Duzee [see type designation] (CAS). **Mexico**—CHIAPAS: 1 ♂, Arriaga, 4 Aug. 1969, L. A. Kelton (CNC); 2 ♂♂, 3 ♀♀, Cintalapa, 3 Aug. 1969, L. A. Kelton (CNC); 19 ♂♂, 26 ♀♀, Comitan, 20 July 1969 & 13 Aug. 1969, L. A. Kelton (CNC); 6 ♂♂, 8 ♀♀, Puerto Arista, 4 Aug. 1969, L. A. Kelton (CNC). DURANGO: 11 ♂♂, 22 ♀♀, 25 mi S Durango, Hwy. 45, 24 July 1964, L. A. Kelton (CNC). GUERRERO: 2 ♂♂, 1 ♀, 20 mi E Acapulco, 10 July 1974, Clark, Murray, Ashe, & Schaffner (TAM). NAYARIT: 1 ♀, Acaponeta, 7 Aug. 1964, L. A. Kelton (CNC). OAXACA: 1 ♀, 11.6 mi W Jalapa de Marques, 12 July 1971, Clark, Murray, Hart, & Schaffner, at light (TAM); 3 ♂♂, 6 mi W Jalapa de Marques, 23 July 1973, Mastro & Schaffner, at light (TAM); 1 ♀, 27 mi NW El Cameron, 24 July 1973, Mastro & Schaffner, at light (TAM); 1 ♀, Jalapa de Marques, 17 Aug. 1969, L. A. Kelton (CNC); 2 ♂♂, 2 mi N Miahuatlan, 14 July 1973, Mastro & Schaffner (TAM); 10 ♂♂, 3 ♀♀, Oaxaca, 21 Aug. 1969, L. A. Kelton, ex. *Hiquerilla* (CNC); 15 ♂♂, 33 ♀♀, Tehuantepec, 28 July 1969, L. A. Kelton (CNC); 1 ♂, 2.1 mi NW Totolapan, 21 July 1974, Clark, Murray, Ashe, & Schaffner (TAM); 1 ♂, Presa Benito Juarez, 23 July 1974, Clark, Murray, Ashe, & Schaffner (TAM). PUEBLA: 1 ♂, Iz. Metamoros, 26 Aug. 1969, L. A. Kelton (CNC). SAN LOUIS POTOSI: 1 ♀, Palitla, 21 July 1970, Schaffner, Murray, & Phelps (TAM). SINALOA: 2 ♀♀, 13 mi E Concordia, 800′, 5 Aug. 1964, L. A. Kelton (CNC); 38 ♂♂, 52 ♀♀, Mazatlan, 6 Aug. 1964, L. A. Kelton (CNC). SONORA: 15 ♂♂, 13 ♀♀, nr. San Jose Beach, 40 mi SW Cd. Obregon, 16–23 May 1961, Howden & Martin (CNC). TAMAULIPAS: 1 ♀, 8 mi W El Limon, 20 July 1970, Murray, Phelps, Hart, & Schaffner, at light (TAM). VERA CRUZ: 8 ♂♂, Vera Cruz, July 1965, N. L. H. Krauss (USNM); 1 ♂, 44 mi W Tampico, 22 Aug. 1967, G. F. Hevel (USNM). **Netherlands Antilles**—6 ♂♂, 3 ♀♀, Curaçāo, Willemstad, Oct. 1950, N. L. H. Krauss (USNM). **Venezuela**—1 ♂, 3 ♀♀, Aragua, Puerto de Cata, 10–11 June 1976, A. S. Menke & D. Vincent (USNM).

Distribution. *P. seriatus* is a widespread species known in Canada and the United

States from Alabama, Arizona, Arkansas, California, Colorado, District of Columbia, Florida, Georgia, Illinois, Kansas, Louisiana, Maryland, Minnesota, Mississippi, Missouri, New Jersey, New Mexico, Nebraska, North Carolina, Oklahoma, South Carolina, Saskatchewan, Texas, Utah, and Mexico (Henry and Wheeler, 1988). I have examined Mexican specimens from the states of Chiapas, Durango, Guerrero, Nayarit, Oaxaca, Puebla, San Louis Potosi, Sinaloa, Sonora, Tamaulipas, and Vera Cruz.

A new United States record is 1 ♂, Nevada, BYU AE NTS, Mercury, 7 Aug. 1965 [no collector data] (USNM).

New records outside of the United States are the Dominican Republic, Honduras, Jamaica, the Netherlands Antilles, and Venezuela.

Hosts. The cotton fleahopper has been recorded from a great number of plants. Hixon (1941) stated that it feeds on 138 species of plants, distributed in 28 families. He added that, in Oklahoma alone, 87 plant species in 24 families are known. Numerous other authors have recorded large numbers of hosts for this polyphagous species (e.g., Reinhard, 1926; Knight, 1926a; Fletcher, 1940; Schuster et al., 1969; Snodgrass et al., 1984).

Although *P. seriatus* has acquired the common name cotton fleahopper, the addition of cotton to its name is somewhat of a misnomer. Despite its importance on cotton, *P. seriatus* prefers a number of other plants over cotton, and seems to move onto this crop only after its preferred host has declined or fleahopper populations have reached proportions that initiate migration.

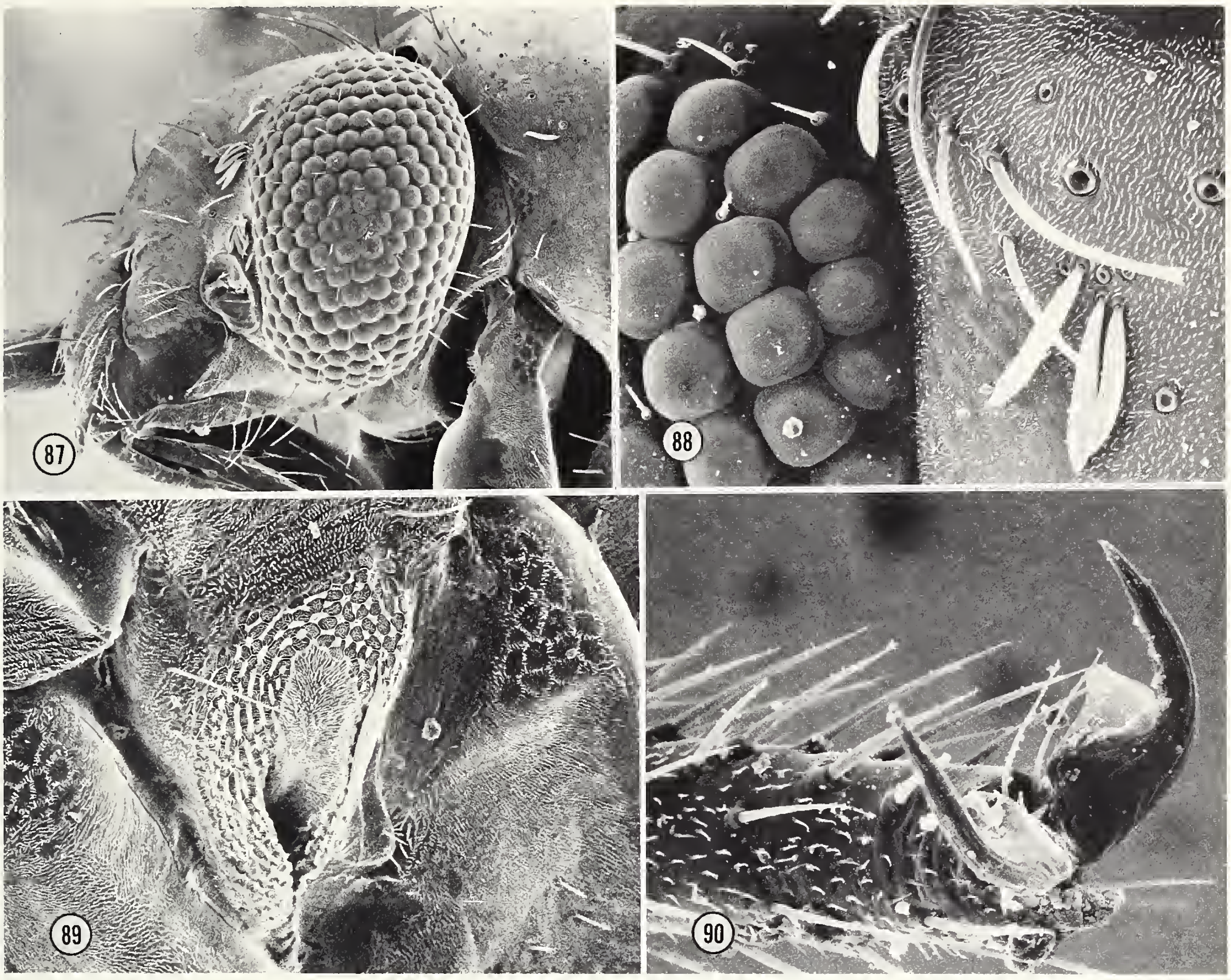
Host genera most commonly associated with *P. seriatus* include (listed alphabetically by family) Amaranthaceae: *Amaranthus* L. and *Tidestromia* Standley; Asteraceae: *Ambrosia* L., *Aster* L., *Conyza* L., *Eupatorium* Bubani, *Gutierrezia* Lag., *Helenium* Adans., *Helianthus* L., *Parthenium* L., *Ratibida* Raf., and *Xanthium* L.; Euphorbiaceae: *Croton* L.; Fabaceae: *Cassia* L.; Lamiaceae: *Monarda* L.; Malvaceae: *Gossypium* L.; Onagraceae: *Oenothera* L. and *Gaura* L.; Polygonaceae: *Polygonum* L.; Solanaceae: *Solanum* L.; and Verbenaceae: *Verbena* L. Of these, species of *Croton, Monarda, Oenothera,* and *Solanum* appear to be among the most common hosts (Hixon, 1941), although large populations can build up on many others. In the American Southwest, species of *Sphaeralcea* [Malvaceae] are the predominant hosts (R. T. Schuh, pers. comm.). In 1981, I collected a large population of *P. seriatus* in the Florida panhandle on shoe buttons, *Syngonathus flavidulus* (Michx.) Ruhl. (Eriocaulaceae), growing along several miles of moist ditches. It would appear that the great polyphagy demonstrated by this species contributes significantly to its broad range from Saskatchewan, Canada to Venezuela, and on many of the Caribbean islands.

TAXON USED FOR OUTGROUP COMPARISON

Lineatopsallus, new genus

Type species: *Psallus biguttulatus* Uhler, 1894.

Diagnosis. Phylinae: Phylini. This new genus is recognized by the overall pale-yellow coloration, clusters of silvery sericeus setae along the inner margin of each eye; the narrow black lines on the 2nd antennal segment, along the dorsal edge of



Figs. 87–90. SEM micrographs of *Lineatopsallus biguttulatus*: 87. Lateral aspect of head (152×). 88. Sericeus setae along inner margin of eye (670×). 89. Ostiolar opening and evaporative area (344×). 90. Pretarsal structure.

each femur, and on the basal half of each tibia; the pale membrane with a dark fuscous mark just posterior to apex of cuneus, and the paler, smoky gray or brown apical areas becoming weakly conspurcate; the black or fuscous spots along the inner margin of the cuneus; and the male genitalia having a slender C-shaped (approaching J-shaped as in some species of *Rhinacloa* Reuter) vesica, a complex left paramere with a short, blunt knob basal to the anterior (left) process, and a peculiar, apically flattened phallotheca.

Description. Generally elongate oval, somewhat delicate, small sized, length from apex of tylus to apex of hemelytral membrane 2.35–3.40 mm; coloration pallid to pale yellow; dorsum impunctate, surface weakly shining; clothed with semierect simple setae, intermixed with clusters or tufts of silvery sericeus setae. Head (Fig. 87) subtriangular in dorsal aspect, frons broadly rounded, more so in females, tylus prominent, somewhat thickened, narrowly rounded apically, antennal segment I surpassing apex by ¼ or less its length, antennal fossa set anteriorly adjacent to lower edge of compound eye at base of emargination, eyes sparsely set with short pale setae; tufts of sericeus setae present at base of jugum, along inner margin of eye (Fig. 88), and across vertex, intermixed with scattered, individual silvery setae. Rostrum extending to metacoxae. Antenna slender, segment I stoutest and shortest, with a dark

inverted L-shaped mark on dorsal and inner surface; segment II uniformly slender, with a distinct fuscous line (interrupted in some specimens) extending entire length; segment III and IV most slender. Pronotum trapeziform, immaculate, with scattered simple and tufts of silvery sericeus setae; calli prominent, contiguous at middle. Hemelytron macropterous, translucent, weakly shiny, with scattered, indistinct, pale-brown spots, set with semierect simple and scattered tufts of silvery sericeus setae; inner margin of cuneus with one to several pale-brown spots (set with only pale, golden-brown setae); membrane translucent pale or white, with a large fuscous spot laterally near apex of cuneus, apical areas weakly clouded with pale brown, some areas becoming indistinctly conspurcate. Legs relatively slender, femora often speckled, dorsal edge of each with a distinct fuscous line dorsally; each tibia with a fuscous "knee" spot and line extending distally to middle or beyond; claws slender, with setiform parempodia and quadrate fleshy pulvilli (Fig. 90). Male genitalia: Vesica very slender, C-shaped, lacking separate spicules, secondary gonopore located at middle; left paramere stout, with a short blunt knob at base of anterior arm; right paramere ovoid, somewhat tapering apically; phallotheca oddly flattened apically.

Etymology. This generic name is derived from the Latin "*linea,*" meaning line, and the mirid generic name "*Psallus,*" to draw attention to the fuscous lines found on the antennae and legs of both included species. The gender is masculine.

Lineatopsallus biguttulatus (Uhler), **New Combination**
Figs. 87–94

Psallus biguttulatus Uhler, 1894:275; Van Duzee, 1917:407; Knight, 1927:35 (in part); Carvalho, 1958:117; Henry and Wheeler, 1988:492.
Oncotylus biguttulatus: Van Duzee, 1923:157.

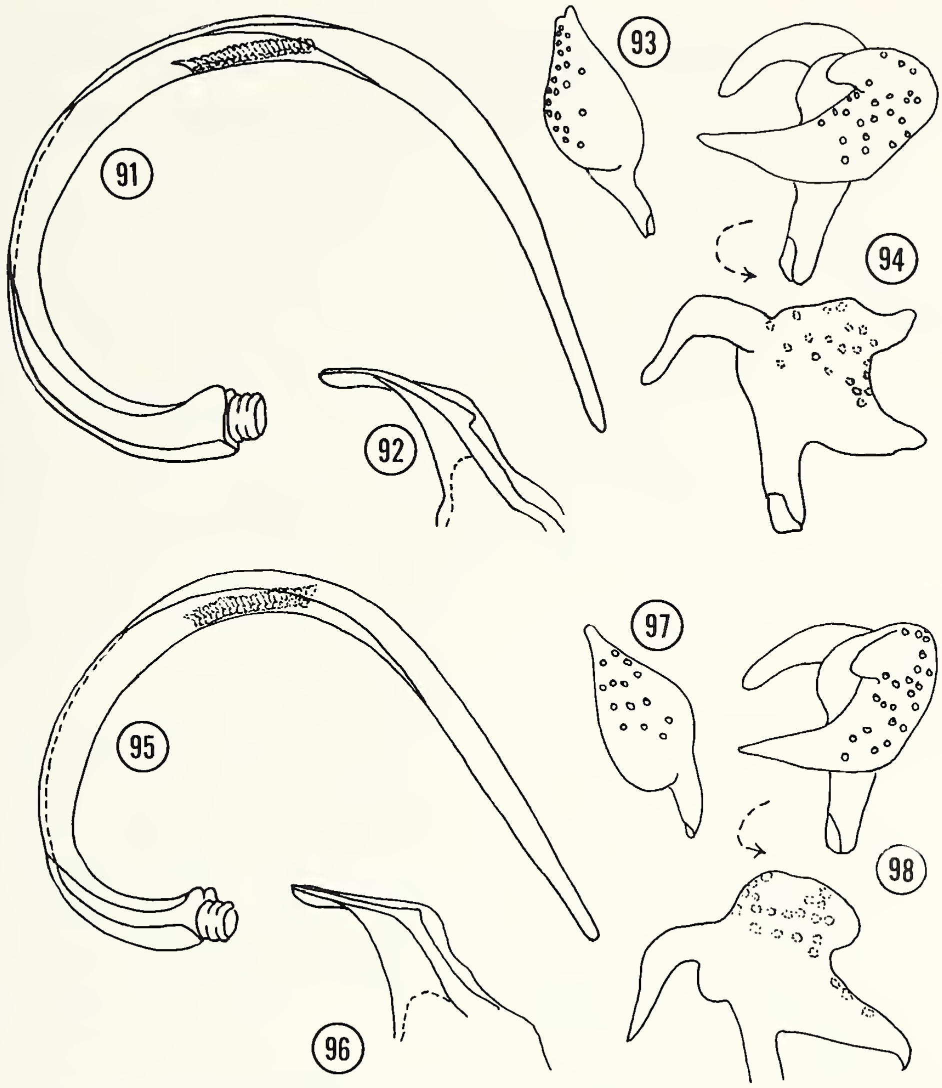
Diagnosis. *L. biguttulatus* is distinguished from *L. slateri* by the larger size, more distinct fuscous lines on the antennal segments and legs, and the larger, more distinct, subapical, fuscous spot on the posterior surface of the meso- and metafemur.

Description. Male (N = 9): Length 2.92–3.20 mm, width 1.16–1.24 mm. *Head:* Width 0.66–0.68 mm, vertex 0.28–0.30 mm. *Rostrum:* Length 1.00–1.04 mm, extending to metacoxae. *Antenna:* Segment I, length 0.22–0.24 mm; II, 0.88–0.92 mm; III, 0.50–0.56 mm; IV, 0.26–0.28 mm. *Pronotum:* Length 0.46–0.48 mm, basal width 1.00–1.04 mm.

Female (N = 14): Length 2.88–3.40 mm, width 1.42–1.62 mm. *Head:* Width 0.66–0.68 mm, vertex 0.36–0.38 mm. *Rostrum:* Length 1.18–1.32 mm, extending to metacoxae. *Antenna:* Segment I, length 0.22–0.24 mm; II, 0.88–0.92 mm; III, 0.50–0.56 mm; IV, 0.26–0.28 mm. *Pronotum:* Length 0.46–0.48 mm, basal width 1.00–1.04 mm.

Female (N = 14): Length 2.88–3.40 mm, width 1.42–1.62 mm. *Head:* Width 0.66–0.68 mm, vertex 0.36–0.38 mm. *Rostrum:* Length 1.18–1.32 mm, extending to metacoxae. *Antenna:* Segment I, length 0.22–0.24 mm; II, 0.88–1.02 mm; III, 0.44–0.48 mm; IV, 0.24–0.26 mm. *Pronotum:* Length 0.48–0.52 mm, basal width 1.06–1.22 mm.

General coloration pallid to very pale yellow, dorsum with erect and semierect



Figs. 91–98. Male genitalia of *Lineatopsallus* spp. *L. biguttulatus*: 91. Vesica. 92. Phallotheca. 93. Right paramere. 94. Left paramere. *L. slateri*: 95–98.

pale to golden-brown simple setae, intermixed with tufts or clumps of silvery sericeus setae. Head (Figs. 87, 88) pale, with scattered pale simple setae and clumps of silvery sericeus setae at base of jugum, along inner margin of eye, and across vertex, frons on some specimens with darker yellow or brownish transverse striations. Antenna pallid; segment I with a distinct, thick, inverted, L-shaped mark on inner margin; segment II with a broad fuscous line extending from base to near apex; segments III and IV pale yellow. Pronotum pale yellow, calli deeper yellow, somewhat more shiny, with scattered silvery sericeus setae, especially across anterior margin. Mesoscutum and scutellum pale yellow. Hemelytron very pale, translucent yellow; setal bases of rubbed specimens giving a finely punctate appearance; most specimens with small, scattered, indistinct brown spots; apex of embolium tinged with brown on some specimens; set with rather long, semierect pale to golden-brown simple setae, intermixed with clumps and scattered individual silvery sericeus setae; inner margin of cuneus (and paracuneus) with 3–4 fuscous spots; membrane translucent white, with a fuscous spot near apex of cuneus, apical area clouded with brown, sometimes broken with pale spots to give a conspurcate appearance. Ventral surface pale yellow; ostiole (Fig. 89). Legs pale; dorsal edge of each femur with a distinct fuscous line, apical half

of anterior face of metafemur with small brown spots, meso- and metafemur with a large, fuscous, subapical spot on posterior side; pro- and mesotibia with a large fuscous "knee" spot and a narrow, fine, fuscous line extending ⅔ length of segment, metafemur with fuscous knee spot and contiguous line continuous to middle of segment; tarsi pale, claws (Fig. 90) brownish.

Male genitalia: Vesica (Fig. 91); phallotheca (Fig. 92); right paramere (Fig. 93); left paramere (Fig. 94).

Type designation. Three syntype females are in the USNM collection. For nomenclatural stability, I select one of two specimens mounted on a single point (female with the dorsal side up) as the lectotype bearing the following labels: 1), "Calmalli Mines, Lower Cal., Mex., Chas. D. Haines, April 1889"; 2), "PR Uhler Collection"; 3) (handwritten), "Psallus biguttulatus Uhler"; 4), "Psallus biguttulatus Uhler [handwritten], Det. Uhler [printed]"; 5) (here added), "Lectotype: ♀ *Psallus biguttulatus* Uhler, by T. J. Henry." This specimen is in good condition, except the left middle leg and antennae are missing, and the dorsum is devoid of most pubescence. The second female on the same point (mounted with ventral side up) and third (bearing same locality data) are considered paralectotypes.

Other specimens examined. Mexico—1 ♀, San Pedro Martir Isl., Gulf of California, April 18, 1921, E. P. Van Duzee (USNM). **United States**—ARIZONA: 1 ♀, [Pinal Co.] Superior, Alt. 2,400 ft, Apr. 16, 1928, A. A. Nichol (USNM); 4 ♂♂, 5 ♀♀, [Presidio Co.] Tinajas Atlas, Apr. 23, 1935, E. D. Ball (USNM). NEW MEXICO: 8 ♂♂, 17 ♀♀, [Dona Ana Co.] Mesilla Pk., Jul. 12, 1927, H. H. Knight (USNM). TEXAS: 1 ♂, 2 ♀♀, [El Paso Co.] El Paso, Jul. 23, 1914, J. C. Bradley (USNM).

Distribution. Known from Calfornia, New Mexico, Texas, and Baja, Mexico (Carvalho, 1958). Arizona is a new state record.

Hosts. Van Duzee (1923) recorded adults and nymphs from *Vaseyanthus insularis* Rose (Cucurbitaceae) on San Pedro Martir Island, Mexico. One specimen in the USNM collection from this locality bears the label "ex. Brandegea," perhaps a misidentification of Van Duzee's published host. Knight's (1927) *Malvaviscus drummondii* record from Brownsville, Texas should be referred to *L. slateri.*

Lineatopsallus slateri, new species
Figs. 95–98

Psallus biguttulatus: Knight, 1927:35 (in part); McGarr, 1933:953.

Diagnosis. *L. slateri* is distinguished from *L. biguttulatus* by the smaller size, the more narrow, often broken or spotted, fuscous lines on the antennae and legs, and the much smaller, fuscous, subapical spot on the anterior surface of the meso- and metafemur.

Description. Male (N = 5): Length 2.36–2.76 mm, width 1.06–1.08 mm. *Head:* Width 0.60–0.62 mm, vertex 0.28–0.30 mm. *Rostrum:* Length 0.96–1.12 mm, extending slightly beyond metacoxae. *Antenna:* Segment I, length 0.18–0.20 mm; II, 0.80–0.84 mm; III, 0.50–0.54 mm; IV, 0.24–0.26 mm. *Pronotum:* Length 0.40–0.42 mm, basal width 0.84–0.86 mm.

Female (N = 11): Length 2.36–2.68 mm, width 1.10–1.16 mm. *Head:* Width 0.56–0.60 mm, vertex 0.32–0.34 mm. *Rostrum:* Length 1.10–1.16 mm, extending to base

of ovipositor. *Antenna:* Segment I, length 0.16–0.18 mm; II, 0.64–0.76 mm; III, 0.44–0.46 mm; IV, 0.24–0.26 mm. *Pronotum:* Length 0.32–0.42 mm, basal width 0.80–0.90 mm.

General coloration pallid to very pale yellow, dorsum with pale, semierect simple setae, intermixed with clumps of silvery sericeus pubescence. Head pale, with scattered pale simple setae and clumps of silvery sericeus setae at base of jugum, along inner margin of eye, and across vertex (as in *L. biguttulatus*). Antenna pale yellow; segment I with a fuscous, inverted, L-shaped mark on inner surface, mark sometimes broken into separate dittolike spots but still forming L-shape; segment II with a narrow, sometimes broken, fuscous line ending distally near apical third of segment; segments III and IV pale. Pronotum pale yellow, calli deeper yellow and more shiny, with scattered clumps of silvery sericeus setae. Mesoscutum and scutellum pale yellow. Hemelytron very pale, translucent yellow, setal bases of rubbed specimens giving a punctate appearance (as in *L. biguttulatus*), some specimens with scattered, indistinct, small brown spots; set with rather long, pale, semierect simple setae and scattered clumps of sericeus setae; inner margin of cuneus (and paracuneus) with indistinct, small brown spots, membrane translucent white, with a fuscous spot near apex of cuneus, apical area usually weakly clouded with brown and sometimes broken to become conspurcate. Ventral surface pale yellow. Legs pale; dorsal edge of each femur with a narrow, sometimes broken, line or, more often, a series of fine linear spots, line on profemur sometimes absent, anterior and sometimes posterior surface finely brown spotted, meso- and metafemur with a small, subapical spot posteriorly (much smaller than on *L. biguttulatus*); tibiae and spines pale, pro- and mesotibia with a fuscous knee spot and narrow fuscous line or series of spots extending to apical third of segments, metatibia with knee spot and contiguous line continuous to near middle of segment, line often incomplete or broken into spots that frequently appear at bases of tibial spines; tarsi pale, claws brownish.

Male genitalia: Vesica (Fig. 95); phallotheca (Fig. 96); right paramere (Fig. 97); left paramere (Fig. 98).

Type specimens. Holotype ♂: United States, Texas, [Cameron Co.] Brownsville, March 26, 1926, T. C. Barber, taken on *Malva.[viscus] drummondii* (USNM). Paratypes: 1 ♂, 3 ♀♀, same data as for holotype (USNM); 2 ♂♂, 7 ♀♀, Texas, Brownsville, April 25, 1925, taken on *Malvaviscus drummondii* (USNM); 2 ♂♂, 1 ♀, Texas, Brownsville, May 10, 1930, R. L. McGarr (USNM).

Etymology. I have the honor of naming this new species after James A. Slater to recognize his career-long accomplishments in systematic entomology. Although I was never one of his students, he has greatly influenced me through the high standards he has set in his own published works. Knowing his early admiration for the Miridae, I feel it is fitting to dedicate this distinctive new species to him.

Remarks. Knight (1927) reported two new state records for *L. biguttulatus.* I have studied his material (USNM) and have discovered that his New Mexico and El Paso, Texas records correctly refer to *L. biguttulatus,* whereas his record from Brownsville, Texas represents *L. slateri.* I also have examined McGarr's (1933) specimens (USNM) from Brownsville reported as *L. biguttatus* and here refer them to *L. slateri.*

Distribution. Known only from Brownsville, Texas.

Hosts. Knight's (1927) host record for *L. biguttatus* from *Malvaviscus drummondii* Torr. & Gray (Malvaceae) should be referred to this species.

Table 1. Character data used in analysis of *Keltonia* and *Pseudatomoscelis.*

Antenna		
1.	0)	Antennal segment I immaculate or with indistinct markings only.
	1)	Antennal segment I with inverted L-shaped mark.
2.	0)	Antennal segment II without dark spots.
	1)	Antennal segment II with 3–5 dark spots.
3.	0)	Antennal segment II without a distinct dark line.
	1)	Antennal segment II with a dark line, usually broken into a series of dots.
	2)	Antennal segment II with a solid dark line.
Head		
4.	0)	Head immaculate, without spots.
	1)	Head distinctly spotted.
5.	0)	Head short, distance from anterior margin of eye to apex of tylus less than ½ total length.
	1)	Head elongate, distance from anterior margin of eye to apex of tylus greater than ½ total length.
Pronotum		
6.	0)	Pronotum immaculate, without spots.
	1)	Pronotum distinctly spotted.
Hemelytra		
7.	0)	Hemelytra without spots.
	1)	Hemelytra with evenly scattered spots.
	2)	Hemelytra with spots coalesced through middle of corium and apex of clavus, surrounded by individual spots.
8.	0)	Hemelytra with evenly scattered spots.
	1)	Hemelytra with a solid central spot, without surrounding individual spots.
9.	0)	Cuneus without dark patches along inner margin bordering membrane.
	1)	Cuneus with dark patches, but without dark bristles.
	2)	Cuneus with dark patches giving rise to dark bristles.
10.	0)	Membrane clear or evenly colored.
	1)	Membrane clouded with pale areas, but not conspurcate.
	2)	Membrane distinctly conspurcate.
11.	0)	Hemelytral membrane without a dark spot near apex of cuneus.
	1)	Hemelytral membrane with a relatively large dark spot near apex of cuneus.
Vestiture		
12.	0)	Head with sericeus setae, but never present in distinct clumps of 3 or more setae.
	1)	Head with clumps of sericeus setae, at least along inner margin of eyes.
	2)	Head with clumps of sericeus setae along inner margin of eyes, as well as clumps arranged in a row along median line.
13.	0)	Pronotum without clumps of sericeus setae.
	1)	Pronotum with scattered clumps of sericeus setae.
	2)	Pronotum with scattered clumps of sericeus setae, as well as clumps arranged in a row along median line.
14.	0)	Hemelytra with sericeus setae, but never in clumps of 3 or more setae.
	1)	Hemelytra with scattered clumps of sericeus setae.
	2)	Hemelytra with scattered clumps of sericeus setae, as well as more concentrated clumps over coalesced spots at middle.

Table 1. Continued.

Legs		
15.	0)	Femora with small dark spots.
	1)	Femora with large dark spots.
16.	0)	Apex of metafemora without stout dark bristles.
	1)	Apex of metafemora along dorsal edge with two or more long, stout, dark bristles.
17.	0)	Metafemora normally slender.
	1)	Metafemora swollen or saltatorial.
18.	0)	Tibiae without spots at bases of spines.
	1)	Tibiae with distinct spots at bases of spines, sometimes fading apically or indistinct on pro- and mesotibiae.
19.	0)	Tibiae without knee spots.
	1)	Tibiae with distinct knee spots.
20.	0)	Tibiae without dark lines.
	1)	Each tibia with a dark line, usually broken into a series of dots, extending distally midway or more.
	2)	Each tibia with a solid line.
Abdomen		
21.	0)	Abdomen immaculate, without spots.
	1)	Abdomen distinctly spotted.
Genitalia		
22.	0)	Vesica not C-shaped.
	1)	Vesica slender, C-shaped.
	2)	Vesica stout, C-shaped, with a visible spicule.
	3)	Vesica stout, C-shaped, with a visible spicule and an apical cuplike process.
23.	0)	Vesica not with a single spicule only (i.e., without a spicule or apex with an apical cuplike process).
	1)	Vesica with spicule, elongate and slender.
	2)	Vesica with spicule, short and stout.
24.	0)	Phallotheca simple apically.
	1)	Phallotheca with a distinct subapical spine.
25.	0)	Phallotheca acute apically.
	1)	Phallotheca apically flattened.
26.	0)	Left paramere without a knob at base of anterior process.
	1)	Left paramere with a distinct knob at base of anterior process.

PHYLOGENETIC ANALYSIS

The data (Table 2) in this study were processed by Hennig86 (Farris, 1988) using the mhennig and ie function that generates trees by implicit enumeration. Analysis of 17 taxa (2 species of *Lineatopsallus,* 12 *Keltonia,* and 3 *Pseudatomoscelis*) and 26 characters (Tables 1, 2) resulted in three equally parsimonious cladograms, each having a length of 40 steps, a consistency index of 92, and a retention index of 95. *Lineatopsallus* was used as the primary outgroup, but a generalized phyline, bearing nontufted sericeus setae, was also included in the analysis to help polarize certain character information. The results support recognition of three monophyletic genera.

Table 2. Character matrix for *Keltonia* and *Pseudatomoscelis* processed by Hennig86.

Characters	123	45	6	11 78901	111 234	111112 567890	2 1	22222 23456
Outgroup	000	00	0	00000	000	000000	0	00000
Lineatopsallus								
slateri	101	00	0	10111	111	000011	0	10011
biguttulatus	102	00	0	10111	111	000012	0	10011
Keltonia								
balli	000	00	0	00221	221	000100	0	30000
bifurca	000	01	0	10221	221	000100	0	30000
clinopodii	000	01	0	20221	222	000100	0	30000
knighti	000	01	0	20221	222	000100	0	30000
mexicana	000	00	0	20221	222	000100	0	30000
pallida	000	01	0	10221	221	000100	0	30000
robusta	000	01	0	10221	221	000100	0	30000
rubrofemorata	000	00	0	11221	111	000100	0	30000
schaffneri	000	01	0	10221	221	000100	0	30000
steineri	000	01	0	10221	221	000100	0	30000
sulphurea	000	01	0	10221	221	000100	0	30000
tuckeri	000	01	0	20221	222	000100	0	30000
Pseudatomoscelis								
flora	010	00	0	00211	111	111100	0	21100
insularis	010	10	1	10211	111	111100	1	22100
seriatus	010	10	1	10211	111	111100	1	21100

The instability in the analysis resulted from a lack of synapomorphies to fully resolve *Keltonia.* The most resolved cladogram (Fig. 99) recognized *K. balli* (at component G), the *sulphurea* group (at component I), and the *tuckeri* group (at component J). Two of the 3 cladograms gave rise at component G to *K. balli* and the distal taxa (the *sulphurea* and *tuckeri* groups). These two cladograms hypothesized a paraphyletic *sulphurea* group, but a monophyletic *tuckeri* group. This instability resulted from the lack of a synapomorphy to define the *sulphurea* group, which may not be monophyletic. The strict (Nelson) consensus tree of these data collapsed the *sulphurea* group into a paraphyletic cluster similar to the latter two cladograms above, but included *K. balli* as well.

Component A defines the taxa treated in this analysis based on the spotted hemelytra, the patchily clouded or conspurcate hemelytral membrane, a dark spot near the apex of the cuneus on the membrane, clumped patches of sericeus setae at least on the head, and the generalized C-shaped vesica.

Component B defines the new genus *Lineatopsallus* by the fuscous lines on the antennae and legs, the unique left paramere, the apically flattened phallotheca, and the slender, C-shaped vesica.

Component C defines the monophyletic grouping of *Pseudatomoscelis* and its sister

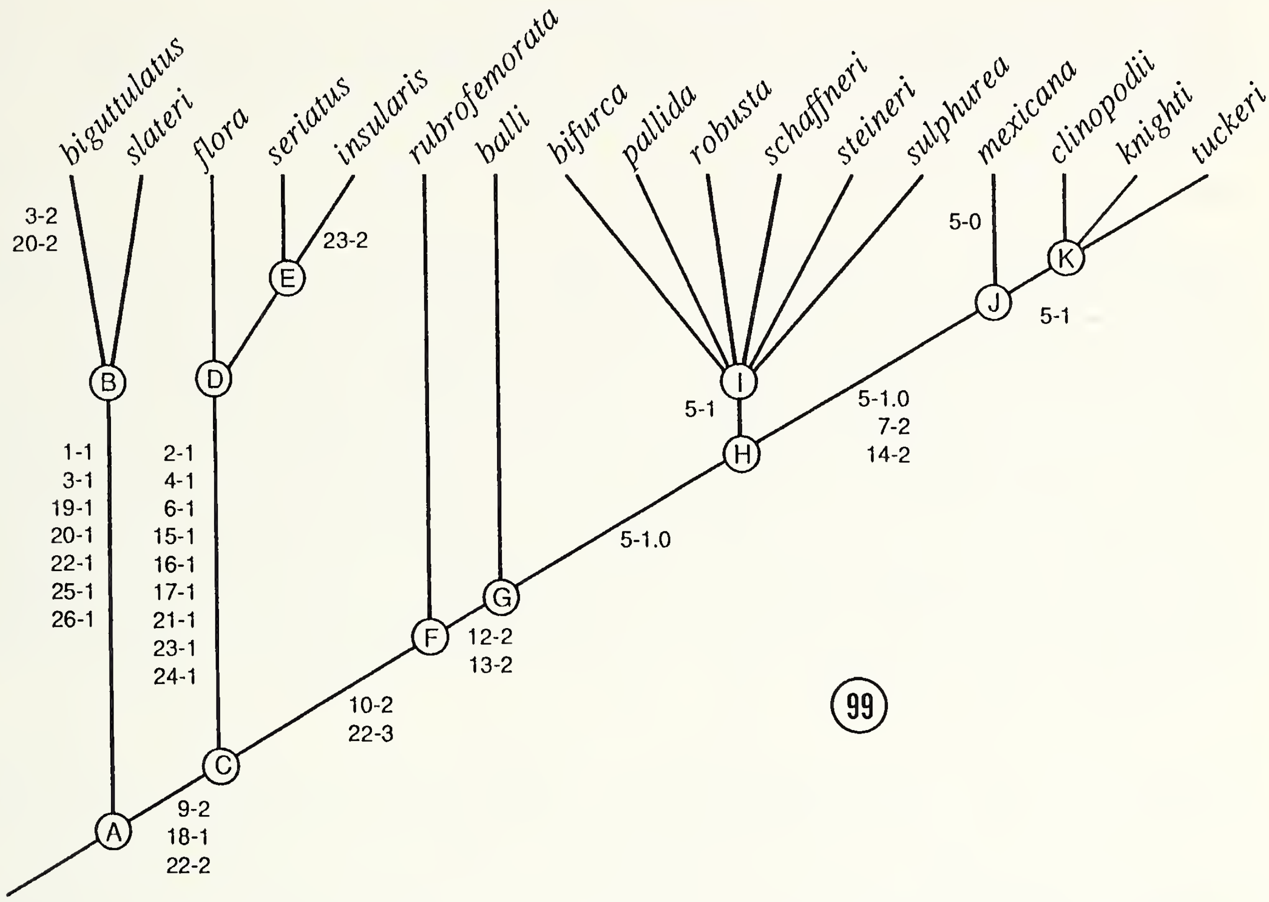


Fig. 99. Most resolved cladogram (one of three) of *Keltonia, Lineatopsallus,* and *Pseudatomoscelis* resulting from character matrix (Table 2) processed by Hennig86. Numbers are characters followed by character states.

genus *Keltonia,* based on the dark, setigerous patches on the inner margin of the cuneus, the distinct tibial spots, and the stout, C-shaped vesica.

Pseudatomoscelis, indicated at component D, is defined by the spotted 2nd antennal segment, saltatorial hind legs with dorsal bristles, and the apically spined phallotheca. Although *P. seriatus* and *P. insularis* are externally quite similar, the vesica type in *P. insularis* is derived relative to that found in *P. flora* and *P. seriatus.*

Component F defines *Keltonia* based the conspurcate hemelytral membrane and the vesica that possesses a cuplike apical process. This clade breaks into four groups: the *rubrofemorata, balli, sulphurea,* and *tuckeri* groups. *Keltonia rubrofemorata* possess a number of autapomorphies (e.g., peculiar solid dark cloud on the hemelytra, shiny dorsum, red femora), but I was unable to find any character information to reveal a further relationship to the remainder of the genus.

Component G defines the remainder of the genus possessing sericeus setae along the midline of the head and pronotum. As with *K. rubrofemorata, K. balli* has several autapomorphies (e.g., pattern of the hemelytra, reddish cuneus), but lacks attributes that would indicate a relationship to the terminal taxa.

Component H depicts the *sulphurea* and *tuckeri* groups. As noted above, it is the instability of these taxa that primarily is responsible for three cladograms. Component I is supported by the derived, elongate head. Although the scattered, hemelytral spotting in *Keltonia* was scored plesiomorphic in relation to *Pseudatomoscelis* and *Lineatopsallus,* it is possible that this type of spotting is not a homologous state, and

may represent an additional synapomorphy for the group. The *tuckeri* group at component J is defined by the pubescent, coalesced spots at the middles of the hemelytra.

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PLANT BUGS OF *QUERCUS ILICIFOLIA*: MYRIADS OF MIRIDS (HETEROPTERA) IN PITCH PINE-SCRUB OAK BARRENS

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Abstract.—An inventory of the Miridae associated with scrub (bear) oak, *Quercus ilicifolia* Wangenh., was conducted in northeastern pitch pine-scrub oak barrens and related natural communities from Maine to Virginia, nearly the complete range of this plant. Samples were taken throughout the season in an extensive pine barren near Frackville, northeastern Pennsylvania. Accounts of the 44 species collected (33 at Frackville) include a review of known distribution and biology, new state records obtained during the study, and data on seasonal history and habits on scrub oak. Three patchily distributed, rarely collected antlike (myrmecomorphic) mirids were discovered: *Pilophorus furvus* Knight, *Schaffneria davisi* Knight, and *S. schaffneri* Knight. These were collected only in or near aphid colonies tended by the ant *Dolichoderus taschenbergi* (Mayr), and they may be Batesian mimics gaining protection from predators because of their resemblance to ants.

The rich fauna of *Q. ilicifolia* consists of phytophagous and predacious mirids, including early-season specialists on staminate catkins, and appears to be more diverse than that occurring on some larger (canopy) oak species. Faunal composition varied among the communities inventoried and, at a given site, changed with seasonal progression. Species richness was greatest in larger pine barrens; few Miridae were collected in remnant pine barrens or in most ridgetop barrens. Several plant bugs are abundant on (but not restricted to) scrub oak, and may be considered indicator species of pine barrens and similar communities.

> How much do we know about life on this little-known planet beneath our feet, the planet earth? We have not even approached the end of cataloguing the creatures that share the earth with us: and this should be the very first step in our knowledge.
>
> —H. E. Evans, *Life on a Little-known Planet,* 1966

Oaks, *Quercus* spp. (Fagaceae), are noted for a rich insect fauna (e.g., Jones, 1959; Southwood, 1960; Elton, 1966; Morris, 1974; Opler, 1974a). Connold (1908), for example, referred to the "vast concourse of dependents" inhabiting British oaks. In addition to such explicit statements, insect diversity of oaks is implicit from host lists of various groups, for instance, those of Patch (1938) for North American aphids and Tietz (1972) for macrolepidoptera. Species richness in North America is particularly developed among cynipid wasps (Felt, 1940; Houard, 1940) and microlepidoptera (Opler, 1974a, b). But great insect diversity (used in the context of numbers of species or richness, not in a strict statistical sense) probably characterizes oaks in all regions with fagaceous forests: eastern and western North America (oaks reach maximum concentration in the Sierra Madres of Mexico), Europe, and Asia (including tropical montane forests).

Among Heteroptera, or true bugs, the diverse mirid fauna associated with oaks in Great Britain and continental Europe is well known (Butler, 1923; Southwood and Leston, 1959; Ehanno, 1965, 1987; Strawinski, 1974; Goula, 1986). Including several plant bugs of presumed accidental occurrence, the fauna collected on *Q. robur* L. in France numbered 36 species; 19 mirids occurred regularly on this plant (Ehanno, 1965).

Miridae associated with North American oaks have received less attention than in Europe, although the number of species known to occur on *Quercus* is considerable (Knight, 1941, 1968; Kelton, 1980). Information on oak plant bugs in North America is mainly limited to lists of species from particular regions, e.g., Illinois (Knight, 1941), and accompanying biological notes; host data cited in taxonomic works treating genera that contain oak-associated species, e.g., *Atractotomus* (Stonedahl, 1990), *Ceratocapsus* (Henry, 1979), *Phytocoris* (Stonedahl, 1988), *Pilophorus* (Schuh and Schwartz, 1988), and *Reuteria* (Henry, 1976); and ecological studies of oak specialists such as *Pseudoxenetus regalis* (Uhler) (Blinn, 1988). In addition, Bray and Triplehorn's (1953) study of insects found on pin oak (*Quercus palustris* Muenchh.) and northern red oak (*Q. rubra* L.) in Delaware includes records of more than 20 mirids, although about half the species should be considered merely incidental on oak. Studies of the plant bug fauna on particular oak species are lacking for North America.

In the mid- to late 1970s, collections from *Q. ilicifolia* Wangenh. in the pine barrens near Frackville, Pennsylvania, suggested that scrub oak harbored a richer plant bug fauna than many tree oaks. Presented here are the results of several years' sampling at this site and an inventory of the mirid fauna of this plant in other areas, mainly northeastern pitch pine-scrub oak barrens. A diverse biota, including endemic rare, threatened, or endangered Lepidoptera, characterizes this globally threatened community type. The requisite conditions of strongly acidic, nutrient-poor soils and natural wildfires rarely occur (Cryan, 1985). Because of fire suppression, housing and industrial development, and other threats, fewer than 20 major pine barrens remain from once extensive occurrences (Cryan, 1985; Schweitzer and Rawinski, 1986). Habitat deterioration is evident in extant barrens (Kerlinger and Doremus, 1981a, b; Schweitzer and Rawinski, 1986; Widoff, 1987).

I am pleased to dedicate this paper to Dr. James A. Slater, world authority on the Heteroptera and respected researcher, teacher, and administrator. Although he became a specialist in the Lygaeidae, he intended to concentrate on Miridae (see Slater, 1978). His early work thus includes several important studies on this group. His encouragement of my biological work on mirids and other Heteroptera, dating from my graduate student years at Cornell University, is genuinely appreciated.

In addition, it seems appropriate here to acknowledge the exemplary efforts of The Nature Conservancy in protecting rare natural communities and species and in helping preserve biodiversity. This paper also is dedicated to TNC and its network of State Natural Heritage Programs, especially to those Heritage and Conservancy staff members who have encouraged and facilitated my faunal inventory work.

STUDY SITES AND METHODS

Description of the natural community. Pine barrens designates a vegetational pattern consisting of open pitch pine (*Pinus rigida* Mill.) forests having an understory

Fig. 1. Pitch pine-scrub oak barrens at Long Pond, Pennsylvania (courtesy Pennsylvania Science Office of The Nature Conservancy).

of heaths and shrubby oaks (Fig. 1). Because the canopy is closed in few places, pine barrens communities technically are woodlands rather than forests (Rawinski, 1987). The name pine barrens, dating from Colonial times, was given to land that would not produce crops and that supported sheep laurel and other plants poisonous to livestock (Cryan, 1985). Sometimes called "devil's land" (Cryan, 1985), pine barrens appear to some as "a sorry collection of small, shrubby, and crowded trees" (Jorgensen, 1978). To others, these bleak wastelands hold a special attraction: "Wastelands [pine barrens], to me, oftentimes seem the least of all wasted" (Teale, 1963).

These shrub-savannah communities (Reschke, 1990) are found in the eastern United States from New Jersey to southern Maine (Olsvig et al., 1979). The well-known New Jersey Pine Barrens sometimes are excluded from the northeastern pitch pine-scrub oak barrens (synonyms of this community type are oak brush plains and pine bush). Because the New Jersey Pine Barrens have a more southern flora, a mosaic of vegetation types unlike those of northeastern pitch pine-scrub oak barrens, and a richer lepidopteran fauna, they may be considered a somewhat different natural community (Schweitzer and Rawinski, 1986). Although pine barrens is a more general term that includes related communities (Whittaker, 1979) such as pitch pine-heath barrens (which lack scrub oaks), this shortened form will be used occasionally in this paper to refer to northeastern pitch pine-scrub oak barrens.

Pine barrens generally occur on sandy, excessively well-drained, nutrient-poor soils. They occur on rolling terrain (but are sometimes flat) ranging from sand dunes to glacial till and outwash plains. Hot by day, barrens experience rapid radiational

cooling at night; depressions in the terrain result in frost pockets that in spring may kill partially expanded foliage of scrub oak. Late-season killing frosts may almost eliminate scrub oak from these depressions (Rawinski, 1987).

In these multilayered communities, pitch pine usually dominates a sparse, interrupted canopy (about 8–16 m high). Scrub oak, *Quercus ilicifolia,* and dwarf chestnut (or dwarf chinkapin) oak, *Q. prinoides* Willd., make up most of the tall shrub layer (about 2–3 m high), often forming a nearly continuous tall shrub canopy. A low shrub layer (0.5 m high or less) consisting of various ericaceous plants (mainly species of *Gaylussacia, Kalmia,* and *Vaccinium*), sweetfern [*Comptonia peregrina* (L.) Coult.], and others is found beneath the tall shrubs and in openings in between. Herbaceous plants account for relatively little biomass but may be present in openings between shrubby thickets. The composition of these grasses and forbs, and their proportion in the community, vary between barrens. Little bluestem [*Schizachyrium scoparium* (Michx.) Nash] often is the dominant grass (Schweitzer and Rawinski, 1986; Widoff, 1987).

Pine barrens are disclimax, fire-dependent communities. They are prone to fire because the underlying sands are rapidly permeable and because high soil acidity retards microbial decomposition of organic matter, which leads to accumulation of a thick layer of duff (Rawinski, 1987). Fires every 6 to 15 years are typical, and a frequency of at least every 15–20 years may be needed to maintain certain pine barrens, that is, to prevent succession to northern mixed forest or other deciduous forest types (Kerlinger & Doremus, 1981a; Cryan, 1985). The frequency necessary for maintenance, however, varies between sites. Where this frequency is low, hardwood trees such as gray birch (*Betula populifolia* Marsh.), aspen (*Populus* spp.), black oak (*Quercus velutina* Lam.), and scarlet oak (*Q. coccinea* Muenchh.) may invade (Schweitzer and Rawinski, 1986; Reschke, 1990).

Several subtypes of pine barrens have been recognized (Schweitzer and Rawinski, 1986). A boreal variant occurs in northern hardwood-spruce-fir regions (northern New York, Maine, and parts of New Hampshire). Various northern herbs are present, but *Q. prinoides* and certain other plants characteristic of more southern pine barrens are absent. In the middle latitudes an inland variant is characterized by colonies of plants such as wild lupine (*Lupinus perennis* L.), New Jersey tea (*Ceanothus americanus* L.), and false indigo [*Baptisia tinctoria* (L.) R. Br.]; examples are the Albany Pine Bush and sites in western Massachusetts, southern New Hampshire, and Rhode Island. Long Island, N.Y., and Cape Cod, Mass., are examples of a coastal variant having an ocean-influenced, moderated climate; these sites have plants such as *Hudsonia* spp. and southern species of Lepidoptera. Barrens in northeastern Pennsylvania, a Poconos variant, have associated wetlands. Fly poison [*Amianthium muscaetoxicum* (Walt.) Gray], rhodora [*Rhododendron canadense* (L.) Torr.], and variable sedge, *Carex polymorpha* Muhl., are present, but plants such as wild lupine and New Jersey tea are absent. Some barrens, such as Scotia in central Pennsylvania (see description of study sites), do not fit any of the above categories (Schweitzer and Rawinski, 1986).

In addition to a distinctive flora, pine barrens are characterized by the presence of animals that do not occur in nearby deciduous forest communities (Cryan, 1980). The New Jersey Pine Barrens (Boyd, 1973) and the Albany Pine Bush (Rittner, 1976) have long been favored collecting grounds for entomologists. Except for Lepidoptera, however, and a few groups such as tiger beetles (Boyd, 1973) and cerambycids

(McCabe and Huether, 1986), the insect fauna of most northeastern pine barrens has not been intensively studied. Characteristic lepidopterans in this community type are the buck moth, *Hemileuca maia* (Drury), a saturniid nearly restricted to feeding on shrubby oaks, mainly *Q. ilicifolia* (Cryan and Dirig, 1975, 1977; Cryan, 1985), and the Karner blue, *Lycaeides melissa samuelis* Nabokov, a lycaenid butterfly that specializes on wild lupine (Dirig, 1976, 1988; Stewart and Ricci, 1988).

Similar, but floristically different, pitch pine-scrub oak associations occur on acidic rocky summits and outcrops (Harshberger, 1911). These ridgetop barrens usually are not as extensive as those in lowland areas. An exception is the Shawangunk Mountains in southeastern New York (see Study sites). Other similar associations are the dwarf pine plains of Long Island, heathlands such as those on Nantucket Island and Martha's Vineyard in Massachusetts (Olsvig, 1980), some serpentine barrens in Maryland and Pennsylvania (Pennell, 1910) and shale barrens of the mid-Appalachians (Platt, 1951), and dry ridges in the southern Appalachians (Schweitzer and Rawinski, 1986).

The host plant. Scrub oak, or bear oak as it is known to foresters (Eyre, 1980), is a scraggly shrub or small round-topped tree belonging to the red oak (subgenus *Erythrobalanus*) group. The numerous tough, crooked, interlacing branches help identify this plant (Brown, 1938). The only other oak likely to be confused with it is the shrubby *Q. prinoides,* which may occur with *Q. ilicifolia* and which locally may also be called scrub oak. It, however, belongs to the white oak group (subgenus *Lepidobalanus*) and can be distinguished by leaves that lack bristle-tipped lobes, a flaky rather than nearly smooth bark, more smooth twigs, more blunt buds, and larger fruit having nut and cup of different form.

Capable of attaining 7–8 m on fertile soil, *Q. ilicifolia* often grows only 1–2 m high. It is especially common on acidic (optimum pH is 4.5 to 6.0), droughty, sterile soils—and thus characteristic of dry sand barrens and rocky hillsides. Scrub oak is shade intolerant, and frequently forms dense, nearly impenetrable thickets. After fire, cutting, or routing, it sprouts vigorously from strong roots and a gnarled, twisted crown (Brown, 1938; Pa. Dep. For. Waters, 1951; Wolgast, 1974). Twenty or more shoots may appear in one clump, and single-stemmed plants have produced as many as 40 stems (Worley et al., 1957).

Quercus ilicifolia usually is said to occur from sea level to an elevation of only 900 m (Eyre et al., 1954), but it is known from about 1,330 m on Panther Knob in West Virginia (Harmon, 1981). Scrub oak ranges from southern Maine through much of southern New England to eastern New York (mainly on Long Island and in the Hudson River valley) and eastern and southwestern Pennsylvania, and south to eastern West Virginia and western Virginia (Fig. 2); scattered populations occur in western North Carolina. In more southern parts of the range, scrub oak is found mainly on eastern slopes of the Appalachians, especially dry slopes of the Alleghenies (Core, 1966). It is particularly common in the anthracite coal region of northeastern Pennsylvania, mainly because of frequent fires and extensive clearcutting (Ineson and Ferree, 1948; Eyre et al., 1954). This plant is characteristic of northeastern pine barrens (Widoff, 1987).

Fruiting is so profuse (more so than in larger oak species) that branches often are covered with clusters of acorns (Pa. Dep. For. Waters, 1951). Sprouts only three years old may bear acorns, although production is greatest when sprouts are 5 to 8 years old. Acorn crops (mast production), which vary from year to year, are adversely

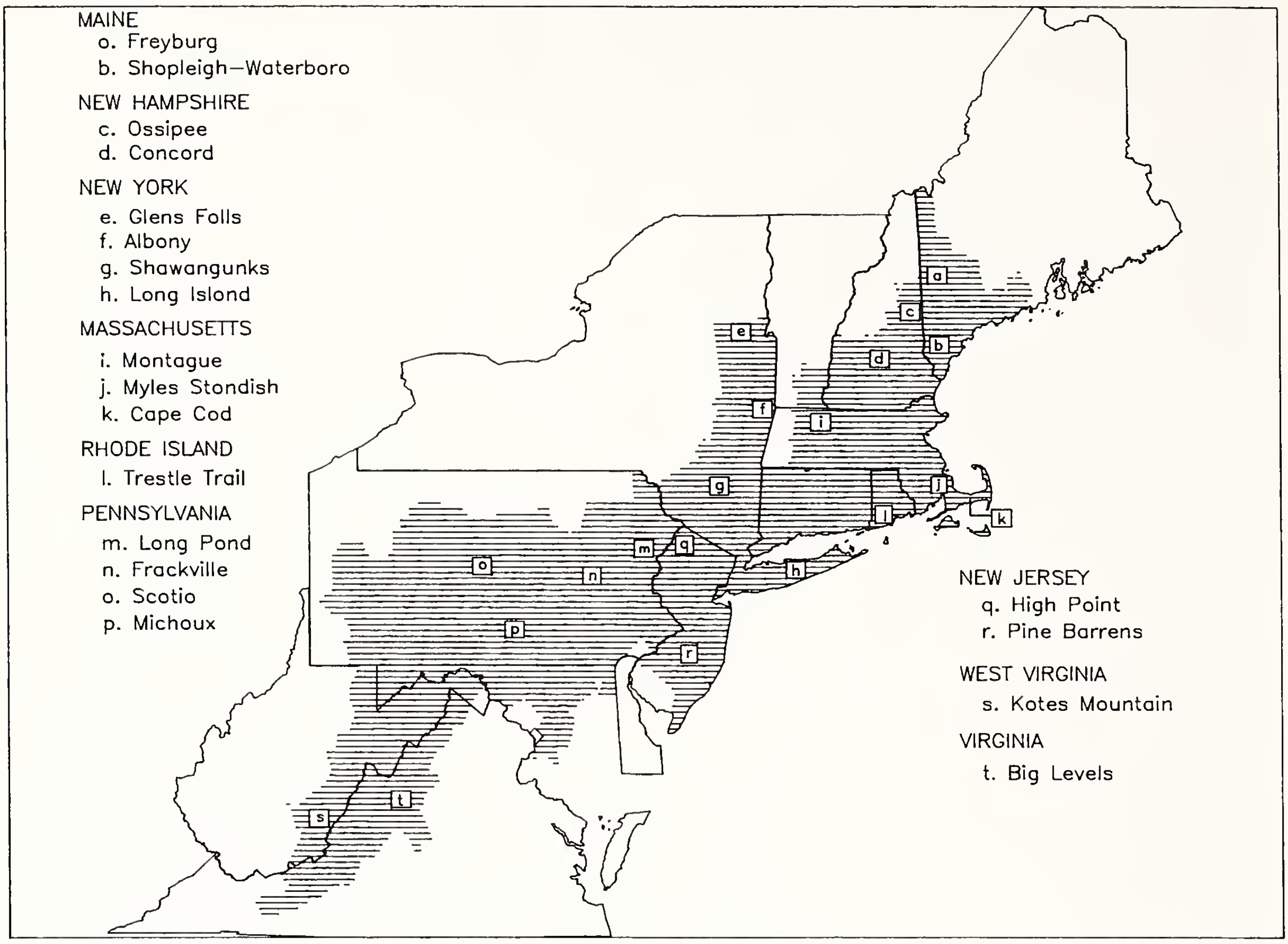

Fig. 2. Distribution of *Quercus ilicifolia* based on Little (1976) (county resolution only, outlier populations omitted) and scrub oak sample sites from Maine to Virginia.

affected by humidity at the time of flowering (Wolgast and Stout, 1977a) and by late spring frosts (Wolgast and Trout, 1979). Genetics also is important in determining acorn yield (Wolgast, 1978).

The importance of scrub oak depends on one's perspective, which is influenced by economic, sociological, and ecological considerations. The tree is too small to be a good timber source, though locally the wood sometimes is used for fuel (Grimm, 1983). And in the early nineteenth century it was used occasionally in New York for fences (Royal Hortic. Soc., 1914). But foresters usually consider scrub oak a troublesome weed because large acreages are rendered unproductive. In areas of frequent fire, it may take 50 years for more valuable tree species to become established. Illick (1924) identified the process of crowding out this noncommercial tree as a major task of modern forestry. With advances in fire protection, forest managers in Pennsylvania could point to substantial reduction in scrub oak forest types: from more than 800,000 ha (2,000,000 acres) in 1920 to only about 69,000 ha (170,000 acres) 30 years later (Pa. Dep. For. Waters, 1951). Attempts at controlling scrub oak have included the use of 2,4, 5-T esters (Worley et al., 1957).

Scrub oak, however, can be considered an important cover plant that protects the forest floor after fires and serves as a nurse crop for valuable trees. It helps prevent erosion and enriches the soil with accumulations of moisture-retaining humus (Pa. Dep. For. Waters, 1951). Rehder (1934) noted its use in covering barren ridges and rocky slopes. *Quercus ilicifolia,* which forms part of a low plant cover along electric

transmission rights-of-way in some areas, is highly resistant to tree seedling invasion and potentially useful in reducing the cost of right-of-way maintenance (Bramble et al., 1990).

Game birds such as turkey, grouse, and quail (Van Dersal, 1938), as well as some nongame birds, feed extensively on the acorns, which represent a highly concentrated food (Wolgast and Stout, 1977b). Bear, deer, and squirrels consume the acorns; deer also browse on the foliage and twigs, particularly in winter when other food is scarce or unavailable (Bramble and Goddard, 1943). Scrub oak is especially important on New Jersey's outer coastal plain, where infertile soils produce little high-quality food for wildlife (Wolgast and Stout, 1977b). In all parts of the range it furnishes cover for a variety of animals throughout the year. Michaux, in fact, thought so highly of the plant as a cover for animals that he (apparently André's son F. A.) recommended it to owners of great estates in Europe (Royal Hortic. Soc., 1914).

Fire exclusion thus can result in deterioration of habitat for wildlife (Hallisey and Wood, 1976). Researchers interested in conserving scrub oak have evaluated the application of fertilizer (and effects of age and stand density) on its reproduction (Wolgast and Stout, 1977b) and investigated the use of prescribed burning to maintain maximum woody browse production for deer (Hallisey and Wood, 1976). One final thought about this plant's value: its ecological importance in "defining and perpetuating the character" (Widoff, 1987) of pine barrens—communities rich in biotic diversity—should be appreciated.

Study sites (Fig. 2). Scrub oak was sampled most intensively in the principal study area: a pine barren in Schuylkill County. Extensive sampling also was conducted at the Long Pond and Scotia barrens (Fig. 2). These Pennsylvania sites are described in some detail, but only brief descriptions of other northeastern pine barrens and similar communities used for inventorying Miridae associated with scrub oak are given.

Frackville (Schuylkill Co.): a moist barren along interstate highway 81 about 8 km southwest of Frackville, elevation about 460 m, apparently fire free for 35–40 years, and the site used by Wheeler and Wilson (1987) to study the little-known issid planthopper *Thionia elliptica* (Germar). They mentioned several plants characteristic of this site; vegetation is similar to that described by Wagner (1943) in scrub oak thickets of Schuylkill Co. and by Donahue (1954) for a scrub oak stand in Luzerne County in Pennsylvania's anthracite region. Mirids at Frackville were sampled along a power line on the east side of the highway.

Lying south of the Poconos, the Frackville site is part of the vast (and probably once continuous) pine barrens region of northeastern Pennsylvania. Forest cover type 43, bear oak, of the American Society of Foresters (Eyre et al., 1954) prevails in the state's anthracite region, mainly in Carbon, Lackawanna, Luzerne, and Monroe counties (Grimm and Whitebread, 1952), and would also include the Frackville study site. Plant communities on these strip-mined areas southwest and west of the Poconos sometimes have been distinguished from barrens within the Pocono Plateau (Oplinger and Halma, 1988).

The northeastern Pennsylvania pine barrens have been little appreciated and seldom cited as communities similar to the New Jersey Pine Barrens, the Albany Pine Bush, or the barrens on Long Island (e.g., Küchler, 1964; Whittaker, 1979). Olsvig et al. (1979) noted the presence of pine barrens in Pennsylvania without mentioning

specific localities. During the 1980s, studies by The Nature Conservancy (Schweitzer and Rawinski, 1986; Widoff, 1987) and the Pennsylvania Natural Diversity Inventory (Wilkinson, 1985) have identified large pine barrens in northeastern Pennsylvania. Although little studied until recently, these communities have been known for many years. Harshberger (1904, 1911) discussed the pine barrens vegetation of northeastern Pennsylvania. He emphasized the close similarity of the "peculiar pine-barren assemblage of species of the mountain floras" of this region, especially in the eastern half of the Pocono Plateau, to the flora of the New Jersey Pine Barrens.

Long Pond (Monroe Co.) (Fig. 1): typical of the Poconos variant (see Description of the natural community), about 2,266 ha on glacial outwash plain just south of Wisconsin terminal moraine, part of a vast semiwilderness that includes boreal wetlands (Wilkinson, 1985). Mirids were sampled mainly in a pitch pine-scrub oak area north of Mud Pond Run and southwest of the village of Long Pond, elev. about 560 m, and in an area southwest near Rt. 115, elev. about 580 m.

Scotia Barrens (Centre Co.): labeled The Great Pine Barrens by an 18th century surveyor (Westerfeld, 1939), about 1,620–2,025 ha of scrub and dwarf chestnut oak, little bluestem and other grasses, scattered pitch pine and aspen, and grassy frost pockets on sandy soil in central part of the Nittany Valley west of State College; wild lupine and northern blazing star (*Liatris borealis* Nutt.) are present; destruction of original oak-chestnut-white pine forest and development of the iron industry with associated railroads, charcoal production, and frequent fires contributed to the vegetation type now present (Westerfeld, 1939, 1959). Mirids were sampled along the main road through State Game Lands No. 176.

Mirids associated with *Quercus ilicifolia* were collected nearly throughout the plant's range (Fig. 2). These additional sites are listed by state, from Maine to Virginia; selected references containing descriptions of the sites and their vegetation are given. In this study, little attention was given to the Long Island and New Jersey pine barrens.

MAINE: pitch pine-scrub oak barrens at Fryeburg, Killick Pond, Shapleigh, and Waterboro in Oxford and York counties (Widoff, 1987).

NEW HAMPSHIRE: pine barrens at Ossipee (Carroll Co.) and remnants of once extensive barrens at Concord, Merrimack Co. (Rawinski, 1987; Cryan, 1985).

MASSACHUSETTS: Cape Cod, Barnstable Co. (Jorgensen, 1978; Olsvig, 1980); Montague Plains, Franklin Co. (Cryan, 1985); and Myles Standish State Forest, Plymouth Co. (Starr, 1926).

RHODE ISLAND: Trestle Trail barrens (Kent Co.) near Connecticut line.

NEW YORK: Glens Falls sand plains, Warren Co. (Cryan, 1985; Reschke, 1990); Albany Pine Bush, Albany Co. (Rittner, 1976, 1980; Olsvig, 1980; Stewart and Rossi, 1981); ridgetop pine barrens at Lake Minnewaska State Park and Mohonk Preserve in Shawangunk Mountains, Ulster Co. (McIntosh, 1959; Kiviat, 1988); and Long Island pine barrens, Suffolk Co. (Cryan, 1980; Olsvig, 1980).

PENNSYLVANIA: ridgetop barrens in Michaux State Forest west of Pine Grove Furnace (Cumberland Co.) and a few small ridgetop barrens not listed in Table 1.

NEW JERSEY: Kittatinny Ridge barrens in High Point State Park, Sussex Co. (Harshberger, 1911; Niering, 1953; Cryan, 1985) and Pine Barrens of southern New Jersey (Harshberger, 1911; Forman, 1979), consisting of a few collections in Burlington and Ocean counties.

WEST VIRGINIA: Kates Mountain shale barren (Keener, 1983) near White Sulphur Springs, Greenbrier Co.

VIRGINIA: Big Levels (Augusta Co.), a quartzite plateau barren at about 1,000 m, similar to northeastern pitch pine-scrub oak barrens but with more tree oaks (T. J. Rawinski, pers. comm.).

Sampling methods. In Pennsylvania, mirids were sampled at Frackville on 5 days from late June to early August 1984, 12 times (weekly or biweekly) from late April to mid-August 1985, 14 times from mid-May to late September 1986, 16 times from late April to late August 1987 (weekly from late April to late July), 4 times from early June to late July 1988, and once (mid-September) in 1990. On each date mirids usually were collected for 30–45 minutes by beating branches of *Q. ilicifolia* over a shallow net and collecting or recording all mirid species and their approximate numbers; notes on plant development also were recorded. Mid- to late instars of taxa that could not be recognized in the field were in many cases reared to maturity in the laboratory. Nymphs were placed in small plastic boxes (about 8 × 2 cm) with twigs (and sometimes staminate flowers or fruits) of the host plant and a water source; presumed predacious species, as well as some phytophages, were provided crushed caterpillars to facilitate rearing. The large number of individuals encountered, however, precluded the rearing of all later instars that could not be field-identified, especially the similar-appearing nymphs of most *Ceratocapsus* and *Phytocoris* spp. Feeding habits of several species were observed in the laboratory.

Pennsylvania barrens at Long Pond and Scotia were sampled less intensively. Collections at Long Pond were made in 1986 (3 days), 1987 (1), and 1990 (2). At Scotia, mirids were collected in 1981 (2 days), 1987 (1), 1988 (1), and 1990 (4). Miridae present on *Q. prinoides,* which is absent from the Frackville and Long Pond barrens, also were noted at Scotia.

Information on Miridae associated with scrub oak in other areas is based on one day's collecting at each site (1–2 hours in August 1990) except for the Albany (New York) Pine Bush (2 days in 1984, 1988) and Maine's Shapleigh-Waterboro barrens (parts of 3 days in August 1990). Voucher specimens have been deposited in the collections of Cornell University, Ithaca, N.Y.; National Museum of Natural History, Washington, D.C.; and Pennsylvania Department of Agriculture, Harrisburg.

RESULTS

Accounts of the Miridae that develop on scrub oak are arranged alphabetically by taxa as in the latest catalog of North American Heteroptera (Henry and Wheeler, 1988). Information provided for the common or characteristic species, as well as some rare or unusual mirids, includes: "Distribution," a summary of the range of widely occurring bugs, or individual records for those known from fewer than 10 states and provinces, and any new state records obtained during this study; and "Biology," a review of selected literature on host plants, seasonal history, and other biological aspects, and any observations obtained from the scrub oak survey. Seldom-collected species for which limited new data can be provided are listed, but only a summary of the known distribution and biology is given, usually in telegraphic form. Table 1 lists all Miridae associated with scrub oak (several *Lygocoris* spp. thought to be vagrants are omitted) and their occurrence in the various communities that were inventoried.

Table 1. Occurrence of Miridae on *Quercus ilicifolia* in pitch pine-scrub oak barrens and similar communities; asterisks denote characteristic scrub oak species.

	ME: Fryeburg	Killick Pond	Shapleigh	Waterboro	MA: Cape Cod	Montague	Myles Standish	NH: Concord	Ossipee	NJ: High Point	Pine Barrens	NY: Albany	Glens Falls	Long Island	Shawangunks	PA: Frackville	Long Pond	Michaux	Scotia	RI: Trestle Tr.	VA: Big Levels	WV: Kates Mtn.
Ceratocapsus																						
*digitulus**	●	●	●	●		●	●	●		●						●	●		●	●	●	
*fasciatus**				●		●							●		●	●					●	●
incisus		●	●	●												●	●					
modestus								●							●							
*pilosulus**			●	●			●			●		●			●	●	●	●				
pumilus										●						●	●					
rubricornis							●				●											
*sericus**			●	●						●						●	●			●		
*vicinus**	●	●	●	●		●	●	●	●	●	●		●	●	●	●	●		●	●	●	●
n. sp.			●																			
Deraeocoris																						
nebulosus				●									●								●	
quercicola			●	●				●				●			●	●	●					
Diaphnocoris																						
provancheri		●		●				●							●	●	●				●	
Eustictus																						
necopinus																			●			
Hyaliodes																						
harti																●	●				●	●
vitripennis[1]										□									●	□		
Lygocoris																						
omnivagus		●	●	●	●	●	●	●				●				●	●		●	●	●	
*semivittatus**				●				●				●				●	●		●			
Noctuocoris																						
fumidus																●						
Phytocoris																						
*antennalis**	●	●	●	●		●	●	●	●	●	●		●		●	●	●		●	●		
canadensis	●	●	●	●		●	●	●		●			●		●	●	●		●	●	●	
erectus									●							●	●					
eximius			●													●			●			

Table 1 (continued)

	ME: Fryeburg	Killick Pond	Shapleigh	Waterboro	MA: Cape Cod	Montague	Myles Standish	NH: Concord	Ossipee	NJ: High Point	Pine Barrens	NY: Albany	Glens Falls	Long Island	Shawangunks	PA: Frackville	Long Pond	Michaux	Scotia	RI: Trestle Tr.	VA: Big Levels	WV: Kates Mtn.
Phytocoris *(cont)*																						
fumatus																●						
husseyi	●															●	●					
lasiomerus												●				●	●		●			
neglectus				●												●						●
*olseni**	●						●				●	●				●	●		●			
purvus			●	●			●			●					●	●						
salicis																●	●					
spicatus																●						
n. sp.															●							
Pilophorus																						
furvus				●		●										●						
neoclavatus			●	●			●	●		●					●	●	●	●	●			
setiger												●					●					
Plagiognathus																						
guttulosus																●						
Psallus																						
variabilis					●									●								
Pseudoxenetus																						
*regalis**					●							●				●						
Reuteria																						
fuscicornis						●													●		●	●
querci		●		●									●						●		●	
Schaffneria																						
*davisi**	●		●	●		●			●		●					●			●			
*schaffneri**				●												●						
Taedia																						
hawleyi				●												●			●			
Teleorhinus																						
*tephrosicola**											●	●		●		●	●		●			

[1]Open squares represent presence of nymphs or field identification of adults; the species involved may be *H. harti.*

Subfamily Deraeocorinae

Tribe Deraeocorini

Deraeocoris nebulosus (Uhler)

A widely distributed (Henry and Wheeler, 1988) predator of various arthropods on ornamental plants, this species sometimes is common on white oak (Wheeler et al., 1975). It was absent from the Frackville site. Nymphs and adults were present on cut-over scrub oak at Glens Falls, New York, in early August, and occasional adults were taken elsewhere (Table 1).

Deraeocoris quercicola Knight

Distribution. Known from Quebec and Ontario south to Georgia and west to Saskatchewan, Colorado, and New Mexico (Henry and Wheeler, 1988). New records are MAINE: York Co., Shapleigh and Waterboro barrens, Aug. 7–9, 1990, and NEW HAMPSHIRE: Merrimack Co., Concord Barrens, Aug. 6, 1990.

Biology. Knight's (1921) type series was collected on white oak (*Quercus alba*) in New York, and the variety *pallens* was described (in part) from specimens taken on bur oak (*Q. macrocarpa* Michx.) in New York. Bray and Triplehorn (1953) reported an adult from either pin or northern red oak in Delaware. Kelton (1980) listed it as an aphid predator on bur oak in the Prairie Provinces. One of the few mirids previously recorded from scrub oak (Wheeler et al., 1983), it also is known from black oak (*Q. velutina* Lam.) and northern pin oak (*Q. ellipsoidalis* E. J. Hill) (Akingbohungbe et al., 1972) and may also breed on hickory (*Carya* spp.) (Knight, 1941; Wheeler et al., 1983).

Unlike *D. nebulosus,* which produces several generations each season and overwinters as an adult, *D. quercicola* is univoltine and overwinters in the egg stage. In the Frackville Barrens, nymphs (first and second instars) were present in late April, fifth instars occurred as early as the first half of June, and adults appeared by mid- to late June. They were present until early August and were taken in mid-August at Long Pond. This common member of the scrub oak fauna was found in several other northeastern pine barrens (Table 1).

Eustictus necopinus Knight

Known from Quebec and Ontario south to Mississippi and west to Manitoba and Missouri (Larochelle, 1984; Henry and Wheeler, 1988). A new record is Pennsylvania (Scotia Barrens). This poorly known, presumably predacious, mirid has been collected at light and on aspen (*Populus*) (Knight, 1923; Kelton, 1980; Blinn and Yonke, 1985). Its association with *Q. ilicifolia* is based on a fifth instar beaten from the trunk or a main branch of scrub oak at Scotia, July 22, 1990.

Tribe Hyaliodini

Hyaliodes harti Knight

Widely distributed in eastern North America and occurring west to the Prairie Provinces and British Columbia (Henry and Wheeler, 1988), *H. harti* has been reported from bur oak in Wisconsin (Akingbohungbe et al., 1972) and the Prairie

Provinces (Kelton, 1980), and white oak in Missouri (Blinn and Yonke, 1985). It is known to be predacious on mites in apple orchards (Gilliatt, 1935) and on other arthropods (Braimah et al., 1982; Kelton, 1982). Nymphs and adults were common on scrub oak only at Big Levels, Virginia (Table 1).

Hyaliodes vitripennis (Say)

The distribution is similar to that of *H. harti* (Henry and Wheeler, 1988). Predacious on mites (Horsburgh, 1969), aphids, and other arthropods (Braimah et al., 1982; Kelton, 1982), it has been collected on northern red oak and pin oak in Delaware (Bray and Triplehorn, 1953) and on northern red oak and white oak in Missouri (Blinn and Yonke, 1985). A few adults were collected on scrub oak (Table 1), and the occasional nymphs encountered (other than at Big Levels, Virginia) may refer to *H. harti* or *H. vitripennis.*

Subfamily Mirinae

Tribe Mirini

Lygocoris omnivagus (Knight)

Distribution. Known from the Maritime Provinces south to Florida and west from Manitoba to Iowa (Henry and Wheeler, 1988).

Biology. In describing this species, Knight (1917) said that it develops on *Quercus alba, Q. coccinea, Q. prinus,* and *Q. velutina,* and less frequently on other shrubs and trees. He observed that nymphs hatch with the unfolding of host buds and feed on tender foliage. In western New York adults appeared during June 10–22, and most died by early August. Other collection records include bur and northern red oak (Kelton, 1982; Wheeler et al., 1983). *Lygocoris omnivagus* sometimes causes catfacing and gummosis of peaches in eastern North America (Rings, 1958 and references therein).

In the Frackville Barrens, nymphs hatched in early May, and mostly third instars were present during mid-to late May. Adults appeared by early June and were present until mid-August. At Scotia, a female was collected as late as mid-September. This univoltine mirid occurred in many of the northeastern pine barrens surveyed in August 1990 and was collected at Big Levels in Virginia (Table 1).

Lygocoris semivittatus (Knight)

Distribution. Recorded from Ontario and Quebec south to Florida and west from Wisconsin and Minnesota to Missouri and Texas (Henry and Wheeler, 1988). New records are MAINE: York Co., Waterboro Barrens, Aug. 7, 1990, and NEW HAMPSHIRE: Merrimack Co., Concord Barrens, Aug. 6, 1990.

Biology. Knight (1917) described *L. semivittatus* from *Q. alba* in New York. Collections from hickory (*Carya*) and willow (*Salix*) (Kelton, 1971; Blinn and Yonke, 1985) may represent dispersal from oaks.

At Frackville, overwintered eggs hatched before vegetative bud break. First and second instars were present on staminate catkins by late April, second through fourth instars by mid-May, and mostly fifth instars by late May. Development of this univoltine, inflorescence feeder is nearly complete by the time staminate catkins

begin to wither. The first adults were collected on May 30 in 1986 and June 3 in 1987. They were abundant through mid-June and present until early or mid-July. Fifth instars and adults were common in the Albany Pine Bush in early June, and a few females were taken during August in other northeastern pine barrens (Table 1).

Phytocoris antennalis Reuter

Distribution. Known from Quebec and Massachusetts south to Florida and west to Iowa and Oklahoma (Larochelle, 1984; Henry and Wheeler, 1988). New records are MAINE: Oxford Co., Fryeburg Barrens, Aug. 10, 1990; York Co., Killick Pond, Aug. 8; Shapleigh Barrens, Aug. 8; Waterboro Barrens, Aug. 7–9, 1990. NEW HAMPSHIRE: Carroll Co., Ossipee Barrens, Aug. 10; Merrimack Co., Concord Barrens, Aug. 6, 1990. RHODE ISLAND: Kent Co., Trestle Trail, near Greene, Aug. 5, 1990.

Biology. Knight (1941) noted that this species is taken most often at light and that it probably is predacious. It has been collected at black light and in a Malaise trap in Missouri (Blinn and Yonke, 1985), and on *Q. rubra* in Quebec (Larochelle, 1984).

Early instars were not recognized among nymphs of other *Phytocoris* spp. occurring on scrub oak in pine barrens. Collection of a third instar at Frackville on July 1, and fifth instars in the Albany Pine Bush on June 30 suggests that the overwintering eggs hatch by early or mid-June. The earliest record of adults at Frackville was mid-July, but fourth and fifth instars usually were found until the end of July. Mid- to late instars also were present during the latter half of August, suggesting that *P. antennalis* is bivoltine. At the Scotia Barrens, adults were present in mid-September. This characteristic pine barrens species (Table 1) typically was collected only from larger branches of scrub oak.

Phytocoris canadensis Van Duzee

Widely distributed in eastern North America (Henry and Wheeler, 1988). A new record is RHODE ISLAND: Kent Co., Trestle Trail, near Greene, Aug. 5, 1990. Known from numerous deciduous trees and shrubs (Knight, 1941; Kelton, 1982; Wheeler et al., 1983) and predacious on lepidopteran eggs, mites, and aphids (Braimah et al., 1982; Kelton, 1982). Late instars and adults were present at Frackville during July and August; adults were collected from early July to early September. It was common at Long Pond and Scotia barrens in Pennsylvania and High Point State Park in New Jersey and was collected in several other northeastern pine barrens and at Big Levels in Virginia (Table 1).

Phytocoris erectus Van Duzee

Occurring throughout much of eastern North America west to Saskatchewan and, perhaps, Utah (Henry and Wheeler, 1988), although Stonedahl (1988) did not list it from western North America. Collected on various deciduous trees and shrubs (Wheeler et al., 1983; Blinn and Yonke, 1985) and predacious on mites, aphids, caterpillars, and lepidopteran eggs (Kelton, 1980, 1982; Braimah et al., 1982). This species was present during August at Frackville and Long Pond. It was less abundant than *P. canadensis* and was taken in fewer pine barrens than that species (Table 1).

Phytocoris eximius Reuter

A wide-ranging eastern North American species (Henry and Wheeler, 1988) whose habits are little known. It was one of the early-appearing *Phytocoris* at Frackville;

late instars were observed in late May through mid-June and adults during late June to late September. Presence of late instars in mid- to late August suggests that *P. eximius* has two generations.

Phytocoris fumatus Reuter

A poorly known species recorded from Massachusetts to Georgia and west to North Dakota (Henry and Wheeler, 1988). A fifth instar of this species (or near) was collected at Frackville in late June.

Phytocoris husseyi Knight

Recorded only from Minnesota, Nova Scotia, Ohio, Pennsylvania, Quebec, and West Virginia (Henry and Wheeler, 1988). A new record is MAINE: Oxford Co., Fryeburg Barrens (E. Brownfield and Clays Pond area), Aug. 10, 1990. Known as a predator of arthropod eggs, mites, aphids, and caterpillars on fruit trees (Braimah et al., 1982; Kelton, 1982), *P. husseyi* was collected occasionally at Frackville and Long Pond from early August to late September. Late instars were present as late as mid-September.

Phytocoris lasiomerus Reuter

A species of transcontinental distribution in the northern United States and southern Canada (Henry and Wheeler, 1988; Stonedahl, 1988). Pennsylvania (Frackville, Long Pond, and Scotia barrens) is a new state record. *Phytocoris lasiomerus* has been collected on herbaceous plants and on apple and other fruit trees where it feeds on mites, mite eggs, aphids, and other small arthropods (Kelton, 1980, 1982; Braimah et al., 1982). Adults, perhaps having dispersed from other plants, were collected on scrub oak at Frackville and Long Pond throughout July; at Scotia, they were present on *Quercus prinoides.* This species also was present on *Q. ilicifolia* in late June in the Albany Pine Bush.

Phytocoris neglectus Knight

Widely distributed from Nova Scotia, Quebec, and Ontario south to Mississippi and west to the Prairie Provinces, British Columbia, and California (Stonehahl, 1988; Henry and Wheeler, 1988). *Phytocoris neglectus* is found on various deciduous trees, including several oak species in Wisconsin (Akingbohungbe et al., 1972), and on conifers, often occurring on bark (Knight, 1941; Stonedahl, 1988). This apparently bivoltine species (Knight, 1941) is predacious on mites, aphids, psyllids, and psocids (Knight, 1941; Braimah et al., 1982; Kelton, 1982). At Frackville, adults were collected on scrub oak from late June to late September; late instars were particularly common during mid- to late August. Fifth instars and adults also were found at the Kates Mountain shale barren in West Virginia (Table 1).

Phytocoris olseni Knight

Distribution. Known from Colorado, Florida, Mississippi, New Jersey, New Mexico, New York, Texas, and Virginia (Henry and Wheeler, 1988). New records are MAINE: Oxford Co., Fryeburg Barrens (Clays Pond area), Aug. 10, 1990. MASSACHUSETTS: Plymouth Co., Myles Standish State Forest, Aug. 5, 1990. PENN-

SYLVANIA: Monroe Co., Long Pond, and Schuylkill Co., Frackville, numerous records during study.

Biology. The habits of *P. olseni* have not been recorded in the eastern United States. Described from the New Jersey Pine Barrens (holotype, Lakehurst) and several localities in the Long Island barrens (Knight, 1923), it is a characteristic species of northeastern pine barrens. It also is common on shrubby oaks in sand scrub habitats in Florida (Wheeler, unpubl.). Knight (1941) placed *olseni* in a phytophagous group of the genus. Oaks are known as hosts in the West, specifically gambel oak (*Q. gambelii* Nutt.) in Colorado (Stonedahl, 1988). Stonedahl, however, noted that western populations of *P. olseni* possibly represent a distinct species.

At Frackville, overwintered eggs of this univoltine mirid hatched in early to mid-May, third instars usually were present by late May, and fifth instars by early or mid-June. Field observations suggest that early instars feed on staminate catkins. The first adults were seen in mid- to late June and were present until mid- or late July; at Long Pond they were collected as late as mid-August. In the Albany Pine Bush, third and fourth instars were found on 10 June, and fifth instars and adults on 30 June.

Phytocoris purvus Knight

Distribution. Reported from District of Columbia, Iowa, Illinois, Maryland, Missouri, North Carolina, South Carolina, and West Virginia (Blinn and Yonke, 1985; Henry and Wheeler, 1988). New records are MAINE: York Co., Shapleigh and Waterboro barrens, Aug. 7–9, 1990. MASSACHUSETTS: Plymouth Co., Myles Standish State Forest, Aug. 5, 1990. NEW JERSEY: Sussex Co., High Point State Park, July 28, 1990. NEW YORK: Ulster Co., Minnewaska State Park, Aug. 3, 1990. PENNSYLVANIA: Schuylkill Co., Frackville Barrens, several collections during study.

Biology. This species, taken mainly at light, has been collected (1 specimen) on bald cypress [*Taxodium distichum* (L.) L. Rich.] in Illinois (Knight, 1941). A Missouri specimen was taken on a sticky board in "oak hickory canopy" (Blinn and Yonke, 1985).

Uncommon at Frackville, *P. purvus* was collected during July and August; fifth instars were taken throughout July. This species was common on scrub oak at High Point State Park in New Jersey and in the Shapleigh-Waterboro barrens in Maine, where late instars and adults were beaten from lichen-covered branches.

Phytocoris salicis Knight

This widely distributed (Henry and Wheeler, 1988) predator of soft-bodied arthropods and their eggs on apple (Braimah et al., 1982), which also is known from other trees and shrubs (Knight, 1941; Wheeler et al., 1983), was seldom taken on scrub oak (Table 1). A few adults were observed at Frackville in early July; they were seen in larger numbers at Long Pond in early July and were present until mid-August.

Phytocoris spicatus Knight

A wide-ranging (Henry and Wheeler, 1988) but poorly known mirid reported from *Quercus alba* in Missouri (Blinn and Yonke, 1985). Pennsylvania (Frackville Barrens) is a new state record. At Frackville, fifth instars were collected in late May and adults

during late June to early July; bivoltinism is suggested by the presence of late instars in late August. An adult also was collected on the bark of white oak at Frackville.

Phytocoris n. sp.

Two adults of an undescribed species (T. J. Henry, pers. comm.) were collected in New York's Shawangunk Mountains: at Lake Minnewaska State Park and at Mohonk Preserve.

Taedia hawleyi (Knight)

This mirine, previously recorded from the District of Columbia, Indiana, Massachusetts, Maine, Maryland, New York, and Ohio (Henry and Wheeler, 1988), has been studied as a pest of hops (*Humulus lupulus* L.) in New York (Hawley, 1917). Late instars and a few adults were collected from withering staminate inflorescences of scrub oak at Scotia Barrens (Pennsylvania is a new state record) in mid-June 1981. This apparent general feeder also was found on inflorescences of shrubs such as *Cornus racemosa* Lam. and *Elaeagnus* sp. at Scotia. At Frackville, *T. hawleyi* developed mainly on *Aronia arbutifolia* (L.) Ell. and only occasional nymphs were seen on scrub oak. An adult was collected from scrub oak in Maine's Waterboro Barrens in August.

Subfamily Orthotylinae

Tribe Ceratocapsini

Ceratocapsus digitulus Knight

Distribution. Known from Quebec and Ontario south to North Carolina and west to Manitoba and Missouri (Henry and Wheeler, 1988). New records are MAINE: Oxford Co., Fryeburg Barrens (E. Brownfield), Aug. 10, 1990; York Co., Killick Pond, Shapleigh, and Waterboro barrens, Aug. 7–9, 1990. NEW HAMPSHIRE: Merrimack Co., Concord Barrens, Aug. 6, 1990. NEW JERSEY: Sussex Co., High Point State Park, July 28, 1990. RHODE ISLAND: Kent Co., Trestle Trail near Greene, Aug. 5, 1990.

Biology. Few host records are available for this poorly known plant bug. It has been taken on sandbar willow (*Salix exigua* Nutt.) in Manitoba (Kelton, 1980) and on fruit trees in Ontario and Quebec (Kelton, 1982); nymphs and adults feed on mites and aphids (Braimah et al., 1982).

Early instars were not recognized among nymphs of *Ceratocapsus* spp. occurring at Frackville. Fourth instars were collected in late June, and the first adults were taken in early July. They were sometimes abundant in mid- to late July and, in most years, were present until late August or early September. This univoltine bug was collected in most northeastern pine barrens and at Big Levels, Virginia (Table 1).

Ceratocapsus fasciatus (Uhler)

Distribution. Widespread in eastern North America from southern Canada to Georgia and known from California and Colorado (Henry and Wheeler, 1988). A new record is MAINE: York Co., Waterboro Barrens, Aug. 7, 1990.

Biology. This species occurs most often on hickory (*Carya* spp.) (Knight, 1923,

1941; pers. obs.) but has been recorded from *Quercus macrocarpa* in Wisconsin (Akingbohungbe et al., 1972); Bray and Triplehorn (1953) took one adult during their survey of *Q. palustris* and *Q. rubra* in Delaware.

Only one adult was collected on scrub oak (late July) at the Frackville site, where the similar-appearing *C. pilosulus* was common. *Ceratocapsus fasciatus,* however, appeared to be characteristic of certain northern pine barrens (Table 1). In early August, late instars and adults were found in New York's Shawangunk Mountains, where this species coexisted on scrub oak with *C. pilosulus.* In Massachusetts, only *C. fasciatus* was present in the inland Montague sand plains, whereas only *C. pilosulus* occurred in Myles Standish State Forest near the coast.

Ceratocapsus incisus Knight

Known from Ontario south to West Virginia and west to Wisconsin and Missouri (Henry and Wheeler, 1988). A new record is MAINE: York Co., Killick Pond, Shapleigh, and Waterboro barrens, Aug. 7–9, 1990. *Ceratocapsus incisus* has been recorded from various fruit trees in Ontario, where it preys on aphids (Kelton, 1982), and from several hardwood trees (Knight, 1941; Wheeler et al., 1983, Blinn and Yonke, 1985). Adults were collected occasionally at Frackville during July and at Long Pond in mid-August; small numbers were present in the Maine barrens listed above.

Ceratocapsus modestus (Uhler)

Widespread in eastern North America from southern Canada to Florida, ranging west to Saskatchewan, Colorado, and New Mexico (Henry and Wheeler, 1988). A new record is NEW HAMPSHIRE: Merrimack Co., Concord Barrens, Aug. 6, 1990. This species occurs on grape (*Vitis* spp.) and various trees, including pin and northern red oak in Delaware (Bray and Triplehorn, 1953), bur oak in Wisconsin (Akingbohungbe et al., 1972) and the Prairie Provinces (Kelton, 1980), five *Quercus* spp. in Pennsylvania (Wheeler and Henry, 1978), and white oak in West Virginia. It is predacious on mites, aphids, whiteflies, and phylloxeran eggs (Wheeler and Henry, 1978; Braimah et al., 1982; Kelton, 1982). This univoltine predator was not taken in Pennsylvania barrens, but a fifth instar was beaten from scrub oak at Minnewaska State Park in New York; two adults were collected in the Concord (N.H.) Barrens.

Ceratocapsus pilosulus Knight

Distribution. Known from Quebec and Ontario south to New York and west to Manitoba (Larochelle, 1984; Henry and Wheeler, 1988). New records are MAINE: York Co., Shapleigh and Waterboro barrens, Aug. 7-9, 1990, and PENNSYLVANIA (Frackville and Long Pond).

Biology. Reported from several tree species, including bur oak in Illinois (Knight, 1941), Wisconsin (Akingbohungbe et al., 1972), and the Prairie Provinces (Kelton, 1980), and known to prey on aphids (Kelton, 1982). At Frackville, fifth instars were collected from mid- to late June, the adults appearing by early July (adults were present in late June in the Albany Pine Bush). Collection of a fifth instar in late August could have represented a second generation or the late hatching of overwintered eggs. This species appeared to be more abundant at Long Pond, where large numbers of adults were observed from early July to mid-August. The latest collection

(Sept. 29) was made at a scrub oak site near Frackville. *Ceratocapsus pilosulus* was found consistently on heavily fruiting trees, a habit of unknown significance but one also reported for this mirid in Quebec (Larochelle, 1984).

Ceratocapsus pumilus (Uhler)

Widespread in eastern North America from southern Canada to Florida and west to Colorado and Kansas (Henry and Wheeler, 1988), found on grape (*Vitis*) and various shrubs and trees (Knight, 1941; Kelton, 1982; Wheeler et al., 1983; Blinn and Yonke, 1985), and predacious on mites and aphids (Braimah et al., 1982; Kelton, 1982). Adults were taken occasionally from late July to mid-August at Frackville and Long Pond; this species also was present at High Point State Park, New Jersey.

Ceratocapsus rubricornis Knight

Known from District of Columbia, Delaware, Illinois, Mississippi, Missouri, Pennsylvania, and West Virginia (Blinn and Yonke, 1985; Henry and Wheeler, 1988). New records are MASSACHUSETTS: Plymouth Co., Myles Standish State Forest, Aug. 5, 1990, and NEW JERSEY: Ocean Co., Rt. 70 nr. Whiting, June 15, 1980. This poorly known bug has been reported mainly from *Quercus* spp. (Henry, 1979), including pin oak and northern red oak in Delaware (Bray and Triplehorn, 1953) and pin oak and willow oak (*Q. phellos* L.) in West Virginia (Wheeler et al., 1983); records from other trees (*Castanea, Tilia*) possibly represent sitting records. Scrub oak collections are limited to the adult noted above from Massachusetts and a third or fourth instar from the New Jersey Pine Barrens.

Ceratocapsus sericus Knight

Distribution. Reported from Illinois, Michigan, New Jersey, New York, Pennsylvania, and Wisconsin (Henry and Wheeler, 1988). New records are MAINE: York Co., Shapleigh and Waterboro barrens, Aug. 7–9, 1990, and RHODE ISLAND: Kent Co., Trestle Trail, near Greene, Aug. 5, 1990.

Biology. Henry (1979) reported northern red oak in Pennsylvania as the first host record for this seldom-collected plant bug. At Frackville, overwintered eggs of this univoltine species hatched in early June, third to fifth instars were found during mid- to late June, and adults began to appear by the first week in July. Adults were present until mid-August, and females have been collected as late as 8 September. This characteristic scrub oak mirid was collected in several other northeastern pine barrens (Table 1).

Ceratocapsus vicinus Knight

Distribution. Illinois, Missouri, New Jersey, New York, Pennsylvania, and West Virginia (Henry and Wheeler, 1988) are the only published records. New records are MAINE: Oxford Co., Fryeburg Barrens, Aug. 10, 1990; York Co., Killick Pond, Shapleigh, and Waterboro barrens, Aug. 7–9, 1990. MASSACHUSETTS: Franklin Co., Montague Plains, Aug. 4, 1990; Plymouth Co., Myles Standish State Forest, Aug. 4, 1990. NEW HAMPSHIRE: Carroll Co., Ossipee Barrens, Aug. 10, 1990; Merrimack Co., Concord Barrens, Aug. 6, 1990. RHODE ISLAND: Kent Co., Trestle Trail nr. Greene, Aug. 5, 1990. VIRGINIA: Augusta Co., Big Levels Barren, Aug. 26, 1990.

Biology. Knight (1923) described *C. vicinus* from Staten Island, New York (holotype), and from well-known pine barrens areas on Long Island (e.g., Yaphank) and in New Jersey (e.g., Lakehurst). Hosts were unknown until Henry (1979) reported it from willow oak in Pennsylvania. At Frackville, first through fourth instars were not distinguished from nymphs of other *Ceratocapsus* spp. Fifth instars were found from early July to early August; adults were present by mid-July, often common from late July to mid-August, and usually could be collected through August. The latest record (a female) was 29 September. Considered a characteristic species of the scrub oak fauna, *C. vicinus* was taken in numerous pine barrens (Table 1) and was the most abundant mirid present in early August at the Concord, Montague, Myles Standish, and Trestle Trail barrens in New England.

Ceratocapsus n. sp.

In Maine, an undescribed species (one male) of the *lutescens* group (T. J. Henry, pers. comm.) was collected in the Shapleigh Barrens. Some species of this group develop on oaks and other deciduous trees, whereas others are pine specialists (Henry, 1979). Studies are needed to determine whether the Maine species is associated with *Quercus.*

Schaffneria davisi (Knight)

Described from the New Jersey Pine Barrens (Lakehurst and Manumuskin) (Knight, 1923), this interesting plant bug is known elsewhere only from Manitoba (Kelton, 1980). New records are MASSACHUSETTS: Franklin Co., Montague Plains, Aug. 4, 1990. MAINE: Oxford Co., Fryeburg Barrens (Clays Pond area), Aug. 10; York Co., Shapleigh and Waterboro barrens, Aug. 7–9, 1990. NEW HAMPSHIRE: Carroll Co., Ossipee Barrens, Aug. 10, 1990. PENNSYLVANIA: Centre Co., Scotia Barrens, July 19, 1990; Schuylkill Co., Frackville Barrens, 1986–90.

Biology. Kelton's (1980) record from bur oak in Manitoba remains the only information on this bug's habits. *Schaffneria davisi* was not found on scrub oak at Frackville until late July 1986. This antlike or myrmecomorphic bug was detected only when collecting on trees colonized by a glossy brownish-black aphid (*Lachnus allegheniensis* McCook) that was tended by a glossy black ant [*Dolichoderus taschenbergi* Mayr)] (Fig. 3). When branches with aphid-infested twigs or leaves were tapped over a net, one or two of the numerous "ants" appeared slightly different; they proved to be *S. davisi.* The mirid also was collected from ant-attended colonies of a tiny yellow aphid [*Myzocallis bella* (Walsh)] on the same or nearby trees. Colonies of both aphids sometimes were found on the same terminal or even same leaf.

It is apparent now why *S. davisi* is so little known, rare in collections, and had not been encountered previously at the main study site. In pine barrens it is always taken with the ant *D. taschenbergi,* which it closely resembles; both are fuscous or nearly so, mostly glabrous, glossy, and of similar size. Distinguishing mirid from ant is difficult when the ratio in the net is 1:50 or 1:100. In addition, colonies of the myrmecophilic *L. allegheniensis,* and apparently also *M. bella,* occur only near nests of *D. taschenbergi* and thus are patchily distributed in a barren. Bradley and Hinks (1968) observed that nests of this ant were absent from habitat areas seemingly identical to those with nests. The scattered nests of *D. taschenbergi* remain in the same

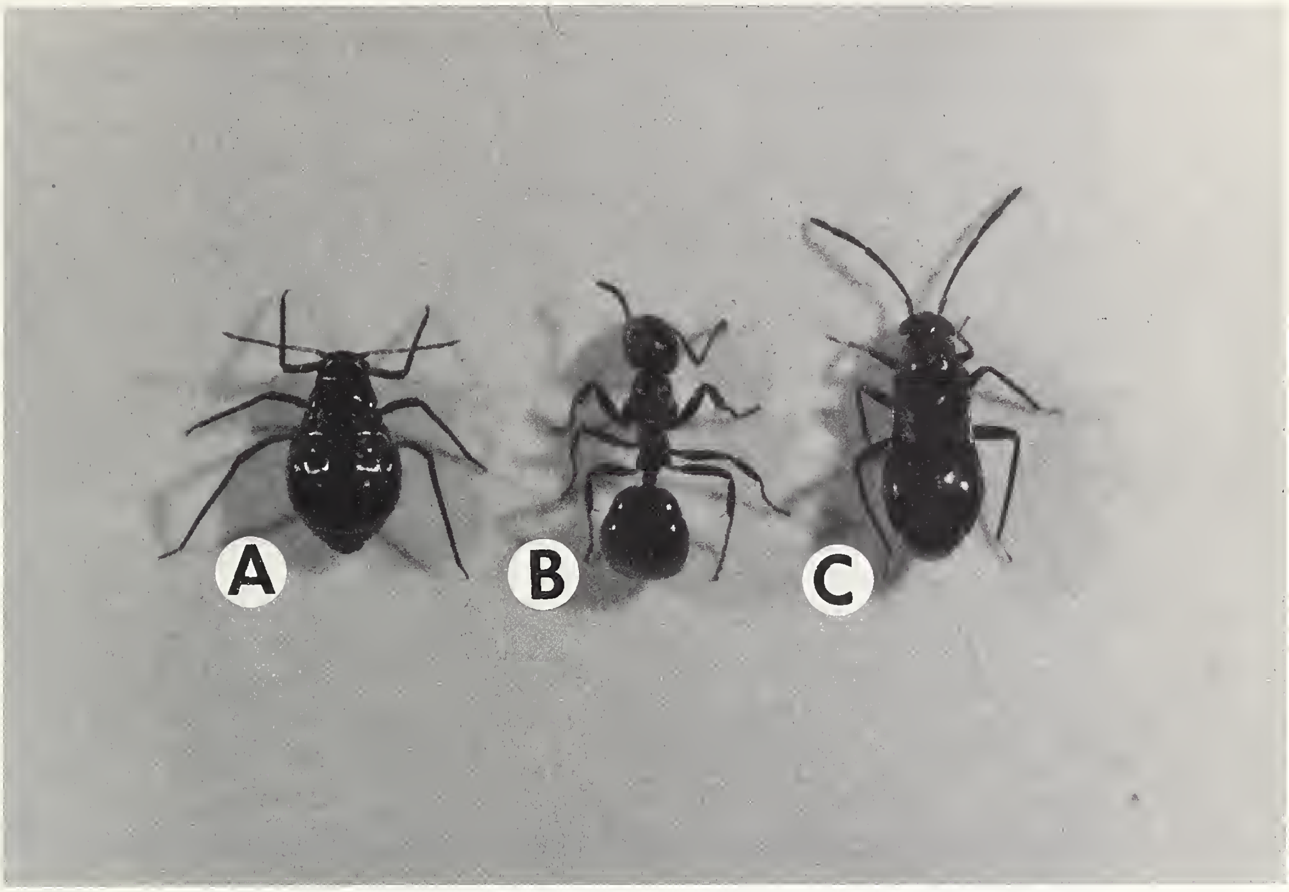

Fig. 3. Members of a presumed Batesian mimicry system on scrub oak. A. The aphid *Lachnus allegheniensis*. B. The ant *Dolichoderus taschenbergi*. C. The myrmecomorphic plant bug *Schaffneria davisi*.

positions year after year (Bradley, 1972), and at Frackville colonies of the aphids *L. allegheniensis* and *M. bella* remained on the same trees in succeeding seasons, a habit noted in other aphid species tended by this ant (Bradley and Hinks, 1968).

The restriction of *S. davisi* to trees harboring aphids and attendant ants—at Frackville and Scotia in Pennsylvania as well as in New England barrens—is hardly coincidental, but the adaptive significance of this relationship within the arthropod community on scrub oak remains untested. Without field or laboratory evidence for a selective advantage of ant resemblance, this apparent ant mimicry is termed myrmecomorphy. It is hypothesized that *S. davisi* derives protection from visual predators that have learned to avoid noxious ants and represents a classic Batesian mimic. Protection of certain ant-resembling heteropterans [*Hyalymenus* spp. (Alydididae) in Brazil] has been experimentally demonstrated (Oliveira, 1985). In Oregon, McIver (1989) has shown that the palatable antlike mirid *Coquillettia insignis* Uhler gains protection from visually oriented predators such as spiders and assassin bugs (Reduviidae) occurring on the bug's host plant.

In addition to its presumed defensive mimicry, seasonal history and habits of *S. davisi* require more study. At Frackville, this plant bug may be bivoltine. Nymphs, mostly third but a few fourth instars, were observed in early June, fifth instars by late June, and the first adults in early July. Adults usually were common during July. Third to fifth instars of a probable second generation were present in mid- to late August, and fifth instars and adults were found through September.

Fig. 4. *Schaffneria davisi* preying on the aphid *Myzocallis bella.*

In the field, nymphs and adults were observed on trunks and main branches near lines of streaming worker ants and on leaves near ant-attended aphids. In the laboratory, *S. davisi* fed on crushed caterpillars. When placed with unattended *Myzocallis* colonies, they aggressively attacked apterous aphids (Fig. 4), usually feeding on several prey in succession. They sometimes deflated their prey, but at times fed briefly, then left a struggling aphid to attack another individual in the colony. When confined with ants and aphids, the mirids were unable to invade the colonies. Ants repelled but did not pursue the bugs, which usually retreated to the underside of a nearby leaf. In nature, the bugs may feed mainly on aphids that stray from colonies, perhaps supplementing this diet with aphid honeydew and scavenging. Ants appear to prevent *S. davisi* from decimating the aphid population. Further study of this possible co-

evolved aphid-ant-plant bug system, including the mirid's use of trail substances or other ant pheromones, is needed.

Schaffneria schaffneri Knight

Distribution. Knight (1966) described this mirid from College Station, Texas, and it has been reported subsequently only from Alberta and Saskatchewan (Kelton, 1980). I note that Kelton's map shows only a record for Saskatchewan and that Henry and Wheeler (1988) inadvertently listed Alberta as Arizona. New records are MAINE: York Co., Waterboro Barrens, Aug. 7, 1990, and PENNSYLVANIA: Schuylkill Co., Frackville Barrens (see discussion below).

Biology. The type specimen and associated material were collected on the ground under red cedar (*Juniperus virginiana* L.) trees; adults and nymphs were observed running and hiding among litter (Knight, 1966). On the basis of observations by M. H. Sweet, Knight said that the bugs may feed on fallen cedar fruits and may be associated with ants. In the Prairie Provinces, Kelton (1980) reported *S. schaffneri* from the grass *Beckmannia syzigachne* (Steud.) Fern.

Schaffneria schaffneri was not as abundant as *S. davisi* at Frackville. In collections of *Schaffneria* adults in 1986, *S. schaffneri* represented 1 of 7 on July 22, 2 of 8 the next day, 3 of 11 on Aug. 1, and 4 of 26 on Aug. 15. Both mirids were collected from the same ant-attended colonies of the aphids *Lachnus allegheniensis* and *Myzocallis bella.* Nymphs presumably were present but were not distinguished from those of *S. davisi.* In Maine's Waterboro Barrens, only one adult was collected, although *S. davisi* was common on scrub oak in certain areas. The comments made about the probable defensive adaptations of *S. davisi* also apply to *S. schaffneri.*

Tribe Orthotylini

Diaphnocoris provancheri (Burque)

Widespread in eastern North America from southern Canada to Georgia, occurring in the Pacific Northwest, California, Colorado, and the Prairie Provinces (Henry and Wheeler, 1988). It is predacious on mites, mite eggs, aphids, leafhoppers, psyllids, and lepidopteran larvae and eggs (Stear, 1925; Braimah et al., 1982; Kelton, 1982) and is found on numerous shrubs and trees, including *Quercus alba, Q. macrocarpa, Q. palustris, Q. prinus,* and *Q. rubra* (Knight, 1941; Kelton, 1980; Wheeler et al., 1983). Adults only were taken in small numbers at Frackville and several other pine barrens (Table 1).

Noctuocoris fumidus (Van Duzee)

Widely distributed across the northern United States and southern Canada, ranging south to Colorado, Utah, and Oklahoma (Schwartz and Stonedahl, 1986). It has been taken at light and on *Carya* and *Quercus* in Canada (Schwartz and Stonedahl, 1986), specifically *Q. macrocarpa* in the Prairie Provinces (Kelton, 1980). Larochelle (1984) collected *N. fumidus* on profusely fruiting oak in Quebec. During the study of scrub oak Miridae, this apparently predacious bug was collected only at Frackville. Small numbers of adults (1–4) were beaten from large branches on each of three sample dates in July 1986.

Pseudoxenetus regalis (Uhler)

Distribution. Reported from Ontario and Quebec south to Florida and west to the Great Lakes region and Oklahoma (Larochelle, 1984; Henry and Wheeler, 1988).

Biology. Blinn's (1988) study of *P. regalis* on white oak in Missouri showed that overwintered eggs hatched shortly after vegetative bud break (early to mid-April), nymphs developed on staminate catkins and tender foliage, adults appeared by early May, and were present only for 3–4 weeks. He noted that this univoltine oak specialist has been collected from other *Quercus* spp., which include members of the red and white oak groups.

At Frackville, egg hatch occurred while staminate catkins were developing but before vegetative bud break on *Q. ilicifolia.* First instars usually were collected during the first week of May, fifth instars about May 20, and the first adults by late May or early June. The somewhat myrmecomorphic nymphs develop rapidly on staminate catkins and perhaps also on expanding foliage. Unlike many of the mirids on scrub oak, egg hatch of *P. regalis* apparently takes place over a short period, and nymphal development is well synchronized; only two instars were present in any sample. Adults were most numerous (sometimes 30–40/sample) in early to mid-June and usually were found until late June or early July. The latest record was July 12.

Pseudoxenetus regalis was one of the most abundant mirids at Frackville and may be characteristic of most pine barrens. Because scrub oak in many other areas was sampled well after the disappearance of this early-season species, few records of *P. regalis* were obtained (Table 1).

Reuteria fuscicornis Knight

Recorded from Ontario south to Maryland and District of Columbia and west to Minnesota, and Iowa (Henry and Wheeler, 1988). This orthotyline has been reported mainly from American hornbeam (*Carpinus carolinianum* Walt.) and hop hornbeam (*Ostrya virginiana* L.), but also from chestnut (*Castanea*) and dogwood (*Cornus*) (Knight, 1941; Henry, 1976). In Pennsylvania, *R. fuscicornis* was found only at the Scotia Barrens where small numbers of adults were taken from late August to mid-September. Because nymphs were not encountered, this species may be incidental on scrub oak, adults having dispersed from their breeding hosts. The collection of large numbers of *R. fuscicornis* from the Big Levels Barrens in Virginia and teneral adults in the Montague (Massachusetts) Plains suggests that *Q. ilicifolia* sometimes serves as a host.

Reuteria querci Knight

Known from New York to Georgia and west to Manitoba and Missouri (Henry and Wheeler, 1988). A new record is MAINE: York Co., Killick Pond and Waterboro barrens, Aug. 7–8, 1990. Bur oak has been recorded as its host in Illinois (Knight, 1941), Wisconsin (Akingbohungbe et al., 1972), and Manitoba (Kelton, 1980); post oak (*Q. stellata* Wangenh.) is a host plant in North Carolina (Henry, 1976). *Reuteria querci* was found at Scotia Barrens, but was absent from the Frackville and Long Pond barrens in Pennsylvania. Fourth and fifth instars were collected in mid-July, fifth instars and teneral adults in late July. Adults were taken in the Glens Falls (New York) sand plains and, as noted above, in Maine barrens; the largest number of adults was collected at the Big Levels, Virginia, site.

Subfamily Phylinae

Tribe Hallodapini

Teleorhinus tephrosicola Knight

Distribution. Described from pine barrens on Long Island, New York (Yaphank), and the New Jersey Pine Barrens (Lakehust) (Knight, 1923), it has been reported since from Missouri and Pennsylvania (Henry and Wheeler, 1988).

Biology. The specific name refers to its apparent host, goat's-rue (*Tephrosia virginiana* L.), a characteristic plant of the Long Island barrens (Cryan, 1980). Late-season collection of the holotype and allotype on flowers of this plant at Yaphank may, however, represent merely a sitting record or dispersal to goat's-rue to feed on nectar or pollen. No other biological information is available on this seldom-collected mirid.

Teleorhinus tephrosicola, although never numerous in samples, was a characteristic scrub oak species at Frackville. First instars were collected as early as May 12, third instars were present by May 20, fifth instars by early June, and the first adults by mid- to late June. Adults were never as common as nymphs on *Q. ilicifolia.* In some years they were observed until late July, but usually they disappeared earlier (a dead adult was beaten from scrub oak on July 15).

The myrmecomorphic nymphs somewhat resemble those of *Pseudoxenetus regalis* but are darker and lack a white or yellowish scutellar spot. Nymphs of *T. tephrosicola* also move much more rapidly over host plants than *P. regalis* nymphs. In the laboratory, nymphs fed on staminate catkins and probed lateral veins and midribs of scrub oak leaves; they fed readily on crushed caterpillars.

In the Albany Pine Bush late instars were observed in early June and an adult in late June. This univoltine mirid also occurred on scrub oak in the Long Pond and Scotia barrens. Early-season collecting is needed to determine whether it is present in New England barrens.

Tribe Phylini

Plagiognathus guttulosus (Reuter)

Distribution. Recorded from Colorado, Florida, Georgia, Illinois, Mississippi, Missouri, and Texas (also known from Mexico) (Henry and Wheeler, 1988). A new record is Pennsylvania (Frackville Barrens).

Biology. Information on host plants is limited to Knight's (1941) record from *Quercus* sp. in Illinois. *Plagiognathus guttulosus* has been collected at light in Illinois and Missouri (Knight, 1941; Blinn and Yonke, 1985).

This early-season inflorescence feeder was encountered only at Frackville. Overwintered eggs hatched in late April when staminate catkins were not fully developed and before leaves unfolded. Third instars were present by mid-May, fifth instars in late May (as early as the 20th), and the first adults in late May or the first week of June. Development takes place rapidly on staminate flowers, and the brownish late instars are well camouflaged on withering catkins. As in *Pseudoxenetus regalis,* populations consist of only one or two instars at any time; all fifth instars become adults within a several-day period. Adults generally were abundant (15–20+ individuals in samples) during mid-June, but their numbers declined quickly. In late June a female

had dispersed to an inflorescence of fly poison, apparently to feed on nectar or pollen. The latest record of this univoltine bug was July 8.

Psallus variabilis (Fallén)

An immigrant species detected in North America on Long Island, New York, in 1979 (Hoebeke, 1980) and later reported from additional localities on Long Island (Wheeler and Hoebeke, 1982). A new record is MASSACHUSETTS: Barnstable Co., North Falmouth, May 28, 1988. On Long Island, nymphs developed on *Q. ilicifolia,* where they appeared to feed mainly on staminate catkins; adults of this adventive mirid have been collected on *Q. coccinea* (Wheeler and Hoebeke, 1982). This early-season, univoltine bug also was collected from scrub oak on Cape Cod, Massachusetts (as noted above), where nymphs were beaten from catkins.

Tribe Pilophorini

Pilophorus furvus Knight

Distribution. Described by Knight (1923) from the New Jersey Pine Barrens (Lakehurst), it is now known to occur in Alabama, Maryland, Mississippi, North Carolina, and Pennsylvania (Schuh and Schwartz, 1988). Schuh and Schwartz did not list the Manitoba record of Bradley and Hinks (1968). Kelton (1980) also did not include *P. furvus* in his Miridae of the Prairie Provinces (he had, however, identified *P. furvus* from Manitoba for Bradley and Hinks), and Henry and Wheeler (1988) said that the Canadian record needed verification. New records are MAINE: York Co., Waterboro Barrens, Aug. 7, 1990, and MASSACHUSETTS: Franklin Co., Montague Plains, Aug. 4, 1990.

Biology. Schuh and Schwartz (1988), on the basis of information I provided for Pennsylvania populations, reported *P. furvus* from Virginia pine (*Pinus virginiana* Mill.) and from *Q. ilicifolia* (Frackville Barrens). If the Manitoba record of Bradley and Hinks (1968) is valid (I am inclined to accept it based on habitat type, their biological data, and the information I have obtained on this species in northeastern pine barrens), then *P. furvus* also lives on jack pine (*P. banksiana* Lam.), on which it attacks *Cinara* aphids that stray from ant-attended colonies.

Like *Schaffneria davisi* and *S. schaffneri, P. furvus* was collected on scrub oak when aphids tended by the ant *Dolichoderus taschenbergi* were located. At Frackville, it was found only in 1987. On July 8, a fourth and a fifth instar were taken with three adults from colonies of the aphid *Lachnus allegheniensis*; a week later, two adults were collected. *Schaffneria davisi* also was present in the same aphid colonies on both dates.

Schuh and Schwartz (1988) pointed out that members of the *P. furvus* species group typically develop on pines and that further field observations would determine whether the Frackville collections from scrub oak represented a breeding record. This species develops on Virginia pine in Pennsylvania and elsewhere in the eastern United States (personal observations), as well as on jack pine in Manitoba (Bradley and Hinks, 1968). Collection of a few adults from *Dolichoderus*-attended aphid colonies on scrub oak in two New England barrens suggests that *P. furvus* belongs to the complex of myrmecomorphic Miridae associated with the aphid-ant-scrub oak sys-

tem. Perhaps the presence of ants and aphids is more important than plant species in determining host relationships of this myrmecomorph.

Pilophorus neoclavatus Schuh & Schwartz

Distribution. Recently described (holotype from Frackville Barrens) for a species long misidentified as *P. clavatus,* an Old World mirid established in parts of North America (Schuh and Schwartz, 1988). This species also has been confused with other North American *Pilophorus* such as *P. brunneus* Poppius. For example, the West Virginia record of *P. brunneus* (Wheeler et al., 1983) should be referred to *P. neoclavatus* (see Schuh and Schwartz, 1988). In describing this species, Schuh and Schwartz recorded it from Ontario and Quebec south to North Carolina and west through the midwest and Great Lakes region to the Prairie Provinces.

Biology. Pilophorus neoclavatus has been collected from shrubs and trees, including *Q. ilicifolia* and *Q. palustris* in Pennsylvania and *Q. stellata* in North Carolina (Schuh and Schwartz, 1988). At Frackville, it was collected consistently but in small numbers (generally <5 individuals per sample date) and usually relatively late in the season. The first nymphs observed were third instars in late June. Adults were present from late June until mid-August. Collection of late instars in early August may indicate that two generations are produced. *Pilophorus clavatus* was collected in several northeastern pine barrens (Table 1).

Pilophorus setiger Knight

Schuh and Schwartz (1988) examined specimens from Illinois, Indiana, Massachusetts, Minnesota, Nebraska, New Jersey, New York, North Dakota, and Pennsylvania (Long Pond Barrens); they were unable to confirm Kelton's (1980) record from Manitoba. It also is known from South Dakota (Knight, 1973). The only host information, except for *Q. ilicifolia* at Long Pond, is a record from *Corylus* sp. (Schuh and Schwartz, 1988). *Pilophorus setiger,* absent from the Frackville Barrens, was common on scrub oak at Long Pond during mid-August (adults and late instars). This species also was collected in the Albany Pine Bush (Table 1).

DISCUSSION

Forty-four species of plant bugs were collected on *Quercus ililcifolia* in pine barrens and in similar natural communities from Maine to Virginia. Species richness varied greatly among the sites inventoried. As might have been expected from island biogeography theory (MacArthur and Wilson, 1967), the number of mirids found on scrub oak was consistently greater in larger barrens such as Frackville (33 species) and Long Pond (21) in Pennsylvania and in Maine's Waterboro Barrens (21). With additional collecting, the Albany Pine Bush, Long Island and New Jersey pine barrens, and Montague Plains and Myles Standish State Forest in Massachusetts almost certainly can be added to this list. In Maine pine barrens, species richness near the northern limit of scrub oak's range was nearly as great as that of any of the communities that were inventoried. The number of species associated with scrub oak at Waterboro might approach that of other barrens if early-season collections are made.

Species richness in remnant pine barrens such as Concord, New Hampshire, and

in most small ridgetop barrens did not approach that of the larger, more floristically diverse pine barrens communities. More intensive collecting in the large ridgetop barrens in the northern Shawangunk Mountains of New York and in the southern Appalachians, especially Big Levels plateau in Virginia, may reveal a mirid fauna nearly as diverse as that of some large northeastern pitch pine-scrub oak barrens.

Scrub oak appears to have a richer plant bug fauna than some larger oak species in eastern North America, although experimental data are needed to confirm this supposition. *Quercus ilicifolia,* as a shrub oak, might have been predicted on the basis of plant structural diversity to harbor a less diverse plant bug fauna than canopy oaks. When plants of similar-sized geographic ranges are compared, insect species richness typically is greater with architecturally more complex plants (Strong et al., 1984). Cornell and Washburn (1979), however, found that the gall wasp fauna of certain shrubby oaks was about as rich as that of some tree oaks.

Diversity of the scrub oak fauna possibly can be attributed to a preference of many plant bugs for open areas. Shrub-and tree-associated species are found more often on isolated trees or on hosts in hedgerows (Knight, 1941; pers. obs.). That the shade-intolerant *Q. ilicifolia* is typical of communities having a sparse, interrupted canopy and often occurs in extensive patches or colonies may therefore contribute to its faunal richness. Scrub oak's tangled, interlacing branches also may provide ideal shelter that allows a diverse predator fauna to develop, particularly bark-inhabiting *Ceratocapsus* and *Phytocoris* spp.

The fauna consists of phytophagous and predacious species and, undoubtedly, mixed feeders that use plant and animal matter. Degree of intimacy with the plant ranges from a few species taken only as adults and which possibly are vagrants that have dispersed from their hosts; those that use *Q. ilicifolia* as an adventitious host, or only in part of their range; to species that occur consistently on scrub oak nearly throughout its range and are characteristic members of its fauna. In the last-named category are the phytophagous *Lygocoris semivittatus* and *Phytocoris olseni,* and the apparently mainly predacious *Ceratocapsus digitulus, C. pilosulus, C. sericus, C. vicinus,* and *Phytocoris antennalis.* Mirids that have been collected at relatively few sites but nonetheless are considered characteristic scrub oak species are the phytophagous *Plagiognathus guttulosus, Pseudoxenetus regalis,* and *Teleorhinus tephrosicola,* and the predacious *Ceratocapsus fasciatus, Schaffneria davisi,* and *S. schaffneri.* Several of these are rarely collected bugs for which biological information has been scant or lacking.

Even the most abundant or characteristic phytophagous members of the fauna probably are not restricted to developing on *Q. ilicifolia.* Most are known from *Q. rubra* and other common species of the red oak group. Oak-associated insects tend to occur on closely related hosts and thus specialize on species of the red or the white oak group (Connor et al., 1980). But several scrub oak Miridae also develop on *Q. prinoides,* a shrubby oak of the subgenus *Lepidobalanus,* when it coexists with *Q. ilicifolia* in certain pine barrens, or they develop on canopy oaks of the white oak group. A higher percentage of oak mirids appears to cross subgeneric lines than do leafmining microlepidoptera (Opler, 1974a, b), leafmining weevils (Connor et al., 1980), or gall wasps (Cornell and Washburn, 1979). Mirids probably are less host specific because even mainly phytophagous species are opportunists that engage in facultative predation (e.g., Wheeler, 1976) and scavenging (e.g., Wheeler, 1971).

Although plant bugs characteristic of scrub oak were present at most sites, faunal composition varied among the pine barrens inventoried. As Strong et al. (1984) emphasized, no colony of a particular plant can be expected to harbor all phytophagous species known to be associated with that plant throughout its range. In their words, "Local communities of phytophagous insects are a variable subset drawn from the regional pool of potential colonists. . . ." Scrub oak not only possesses a rich phytophagous mirid fauna but is a host of numerous predacious species. Composition of this predatory fauna presumably is influenced by the presence and density of canopy oaks and other hardwoods occurring in pine barrens.

Faunal composition at Frackville, the only pine barren sampled regularly, changed as the season progressed. Mirids specializing on staminate catkins, or at least appearing to feed extensively on this temporary resource, were among the first to appear. Egg hatch of the univoltine *Lygocoris semivittatus, Plagiognathus guttulosus,* and *Pseudoxenetus regalis* occurred in late April or early May before vegetative bud break. Eggs of the univoltine predator *Deraeocoris quercicola* also hatched before leaves unfolded. Although early-season collections may yield only three or four species, it is possible to collect 15 to 20 species at a given time during July or August. In Maine's contiguous Shapleigh and Waterboro barrens, 22 species were taken during portions of three days in early August. Predacious mirids such as univoltine *Ceratocapsus* spp. and bivoltine *Phytocoris* spp. tend to dominate late-season collections.

An analysis of mirid distributional patterns, including origin of the fauna, is premature because of inadequate sampling of northeastern pine barrens and similar communities, and because of a fragmentary knowledge of mirid distribution in North America. Table 1 suggests that the fauna of the communities sampled corresponds somewhat with the major pine barrens variants: boreal, inland midlatitude, coastal, Poconos, and unclassified. Several species of more southern range that are known from the New Jersey Pine Barrens and Long Island barrens, e.g., *Phytocoris olseni* and *Teleorhinus tephrosicola,* were found in the Albany Pine Bush. Some Lepidoptera reach their northern limit at Albany (Schweitzer and Rawinski, 1986), as do certain amphibians and reptiles (Stewart and Rossi, 1981). *Phytocoris olseni* and another species of apparent southern range, *Ceratocapsus rubricornis,* occur in the Myles Standish State Forest, a coastal barren in Massachusetts. Presence of *P. olseni* in the northernmost major pitch pine-scrub oak barren, Maine's Fryeburg Barrens, however, was unexpected.

No remarkable boreal elements were present in Maine barrens; this may reflect lateness of the collecting, but a scarcity of northern species of Lepidoptera also is typical of Maine pine barrens (Widoff, 1987). Two mirids of northern range, *Noctuocoris fumidus* and *Phytocoris lasiomerus,* were collected in Pennsylvania's Frackville Barrens; the latter species also occurred at Scotia Barrens. Schweitzer and Rawinski (1986) noted that Scotia belongs to a group of barrens difficult to categorize. The only specimen of *Eustictus necopinus* taken during the study was from Scotia, and the only *Reuteria* spp. found in Pennsylvania barrens also were collected there.

Two undescribed mirids of undetermined association with scrub oak were collected during the study. Perhaps most interesting, however, was the discovery of an aphid-ant-plant bug system that includes the myrmecomorphic *Schaffneria davisi, S. schaffneri,* and *Pilophorus furvus* as probable Batesian mimics receiving protection from predators because of their resemblance to ants. How this system functions within

the arthropod community associated with scrub oak and the possible coevolution of the mirids with ant-attended aphids are points worth investigating.

Numerous other questions remain unanswered regarding the diverse mirid fauna of *Quercus ilicifolia* in pitch pine-scrub oak barrens. What is the critical size of these ecological islands necessary to maintain species diversity? How does early-season frost damage affect plant bugs? A more crucial question concerns the effects of fire on the mirid fauna. Pine barrens organisms generally are fire-adapted, but most arboreal plant bugs overwinter in the egg stage. They could be severely affected by fire. Ant mimetic bugs such as *Schaffneria* spp. and *Pilophorus furvus* appear to depend on the presence of aphid colonies tended by the ant *Dolichoderus taschenbergi*. Fire, however, destroys colonies of this ant, and its natural rate of spread is slow (Bradley, 1972). Therefore, the presence of these poorly known, patchily distributed and, perhaps, rare myrmecomorphic mirids should be considered when prescribed burning is used to manage pine barrens.

The impressive number of Miridae occurring on *Q. ilicifolia* further documents the biodiversity associated with pitch pine-scrub oak barrens. Several plant bugs, including *Schaffneria* spp., not only appear to be characteristic of scrub oak but indicators of pine barrens or other sand scrub habitats. As such, certain mirids might serve as barometers of the health or vitality of a particular pine barren. These unique natural communities, and their associated biota, deserve to be appreciated and preserved.

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A SURVEY OF MALE GENITALIA IN LETHAEINE GENERA (HETEROPTERA: LYGAEIDAE: RHYPAROCHROMINAE)

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Abstract.—The clasper and sperm reservoir of 50 species in 31 genera are described, and most are figured. The sperm reservoir, and to a lesser extent the clasper, exhibit a wide variety of form. A preliminary assessment of the taxonomic value of these structures indicates that they are important at several taxonomic levels. These structures are useful in distinguishing externally similar species. Synapomorphies in these structures indicate that some genera are monophyletic, but that other genera are clearly composite and in need of review. Genera are also combined into related groups based on putative apomorphic characters. *Bocundostethus* Scudder, *Kinundastethus* Scudder, and *Microlugenocoris* Scudder are transferred from the Lethaeini to the Antillocorini because they lack synapomorphies characteristic of the Lethaeini.

This study examines characters of the male genitalia, specifically the clasper and sperm reservoir, in the lygaeid tribe Lethaeini (Rhyparochrominae), in order to assess the amount of variation present among genera and species, and to determine the utility of these characters in taxonomic and phylogenetic studies of the tribe. The Lethaeini is an ideal group for a study of this type because the tribe is undoubtedly monophyletic (Ashlock, 1964; Slater and Woodward, 1982), based on the following synapomorphies: linear placement of trichobothria on abdominal sternum five, loss of the y-chromosome, extreme modification of the sperm reservoir, and development of "iridescent" head areas. Out-group comparisons are possible because the sister-group of the Lethaeini has been hypothesized to be the Lilliputocorini; members of both tribes share a reduced dorsal abdominal scent gland in the nymph (Slater and Woodward, 1982). The tribe Antillocorini is the sister-group of the Lethaeini + Lilliputocorini (Slater and Woodward, 1982), providing another out-group.

It became apparent at the outset of this study that 3 African genera described by Scudder (1962) (*Bocundostethus,* with 2 species; *Kinundastethus,* monotypic; and *Microlugenocoris,* monotypic) and placed in the Lethaeini *sensu lato* at that time, actually belong in the related tribe, Antillocorini. They exhibit none of the characteristic lethaeine synapomorphies listed above, and are hereby transferred.

Hemipterists have a long tradition of studying genitalia. In fact, it is particularly appropriate that this paper honor James Slater, since his doctoral thesis was on female genitalia as taxonomic characters in the Miridae (Slater, 1950), and since he has subsequently used both female and male genitalia extensively in his numerous taxonomic studies of the Lygaeidae (see for example Slater, 1979).

While some lygaeid taxonomists have used characters of the entire phallus (Ashlock, 1957, 1964; Harrington, 1980; Malipatil, 1978; Slater, 1985; Sweet, 1967), the present work focuses on just two parts of the phallus, the clasper and the sperm

reservoir. Claspers have traditionally and routinely been used to distinguish between externally very similar species (Slater and O'Donnell, 1979, is just one example), and are generally regarded as species-specific. The sperm reservoir, however, which is the most conspicuous feature of the lethaeine phallus, has been underutilized in taxonomic studies, usually figured incidental to a species or genus description. The comparative approach employed here has been used in other lygaeid subfamilies (Slater, 1979, for the Blissinae, and Slater, 1985, for Australian Lygaeinae), but not yet extensively in the Rhyparochrominae. This first attempt indicates that much taxonomically useful information can be obtained relatively easily.

General morphology of lygaeid male genitalia has been detailed by Bonhag and Wick (1953), Dupuis (1955, 1970), and Ashlock (1957). The following summary deals more specifically with the clasper and sperm reservoir, and with peculiarities of lethaeine genitalia. The claspers and phallus are borne in a cup-like genital capsule (=pygophore) derived from the ninth abdominal segment. The paired symmetrical claspers sit in sockets in the dorsal opening of the capsule. In order to facilitate discussion of the variation among claspers, the following terms are used to designate particular areas of the clasper (Fig. 142).

Blade: the distal curved portion of the clasper; equivalent to "blade" of Ashlock (several papers), Slater and Harrington (1970); and "hook" of Slater and Sweet (1977).

Shank: the basal area of the clasper, between the area of attachment and the blade; equivalent to "shank" of Ashlock (1957) and Slater and Harrington (1970); and "base" of Slater and Sweet (1977).

Area of attachment (Slater and Harrington, 1970): The most basal portion of the shank, where the clasper is attached to the membrane, visible as an opening; equivalent to "basis parameri" of Dupuis (1955) and Ashlock (1957). Frequently a flange (Slater and Sweet, 1977) is present, and the area of attachment is often prolonged laterally.

Inner projection: the projection of the median (relative to insect) curve of the clasper, at the junction of the blade and shank; often with an expanded "mesal" portion that projects "up" from the major plane of the clasper.

Outer projection (Slater and Harrington, 1970): the projection of the outer (relative to insect) curve of the blade, where the expanded basal portion joins the shank. The outer projection is usually broadly rounded in the Lethaeini.

The phallus itself, which appears when inflated as an elongate sheath surrounding a central tube (the endophallus or seminal duct), consists of two parts, a sclerotized phallotheca into which the rest of the phallus fits when not inflated, and the endosoma Ashlock (1957). The endosoma is further divided into a proximal conjunctiva and a distal vesica. The sperm reservoir is located at the proximal end of the vesica and is permanently fixed to its dorsal wall (Ashlock, 1957).

Various authors have used different terms for the structure referred to in this paper as either "sperm reservoir" or "ejaculatory reservoir." The following is a list of equivalent terms: endophallic sperm reservoir (Bonhag and Wick, 1953); conducting chamber (Kumar, 1964); seminal chamber (Sweet, 1967). Dupuis (1955) and Ashlock (1957, 1964) use "ejaculatory reservoir," and Slater and Harrington (1970), Slater and O'Donnell (1978) and several recent authors use "sperm reservoir."

The lethaeine sperm reservoir consists of parts of uncertain homology. Terminology for these parts follows Woodward and O'Donnell (1988), expanding upon initial

attempts by Slater and O'Donnell (1978). The following parts make up the sperm reservoir of lethaeine lygaeids (Figs. 143, 144):

The *conjunctival seminal duct* is that portion of the seminal duct that runs through the lumen of the conjunctiva and into the sperm reservoir. It is equivalent to "ductus seminis conjunctivae" (Ashlock, 1957); "ductus seminis proximalis" (Dupuis, 1970); "the part of the endophallus which leads to the sperm reservoir" (Bonhag and Wick, 1953); and "reservoir duct" (Woodward and Malipatil, 1977), and is undoubtedly homologous across the Lygaeidae.

The *vesical seminal duct* is that portion of the endophallus (seminal duct) which exits the sperm reservoir and continues through the vesica to terminate at the gonopore. It is equivalent to "ductus seminis visicae" (*sic*) (Ashlock, 1957); "ductus seminis distalis" (Dupuis, 1970); "ejaculatory duct" (Slater and O'Donnell, 1978); and "the portion of the endophallus leaving the endophallic sperm reservoir" (Bonhag and Wick, 1953). In lethaeines, the proximal portion of the vesical seminal duct is highly pigmented (=strongly sclerotized) and is treated in this paper as part of the sperm reservoir proper. This part of the vesical seminal duct has been called the "neck" by Ashlock (1957), but since this term has been used to describe what is probably not a homologous structure in other lygaeid sperm reservoirs, it is inappropriate.

The *wings, holding sclerites* and *membranous bulb* are all used in the sense of Ashlock (1957), since each is probably homologous with the structure bearing the same name in other groups.

The *sleeve* is the sclerotized outer wall of the sperm reservoir. It is equivalent to the "sclerotized cylinder" of Slater and O'Donnell (1978), who believed it developed from a basal spur present in other lygaeid sperm reservoirs. I now believe that the sleeve is actually the outer wall of the vesica, which has become sclerotized and rather rigidly associated with the sperm reservoir. The sleeve is often partially surrounded by *corrugations*. Homology of these corrugations is uncertain.

The *arcuate extension* is the curving projection that starts at the insertion of the conjunctival seminal duct and extends to varying degrees around the membranous bulb, often dividing it into two separate lobes. A projection from the opposite side of the opening of the vesical seminal duct may extend outward to meet the arcuate extension. The sleeve connects to the base of the arcuate extension near the conjunctival seminal duct. The arcuate extension has no obvious homolog in other Lygaeidae.

MATERIALS AND METHODS

Fifty species (out of a total of 154 in the Lethaeini) in 31 genera (out of 37 in the Lethaeini) were dissected. Numbers in parentheses after "Species examined" in the Results refer to the number of species studied out of the total number of described species in that genus. In most cases a single individual of each species was dissected. Male genitalia of *Stictolethaeus slateri* O'Donnell are figured in its recent description (O'Donnell, 1991). Males of the following monotypic genera were not available for study: *Carabocoris* Gross, *Lethaeograndellus* Scudder, *Lispolophus* Bergroth, *Orbellis* Distant and *Porrectolethaeus* Scudder. References to original descriptions and subsequent taxonomic changes are given in Slater's (1964) catalog and its forthcoming addendum (Slater and O'Donnell, unpubl.).

Abbreviations in parentheses following locality data refer to the following collections, from which specimens were borrowed: JAS = James A. Slater collection, The University of Connecticut; BM = British Museum (Natural History); QSLD = University of Queensland, Brisbane, Australia.

All observations, dissections and drawings were done with a Leitz-Wetzlar binocular dissecting microscope. Drawings were done at 64× or 160× with the aid of an ocular grid.

Male specimens chosen for dissection were softened for 5–8 minutes in a few drops of relaxing fluid (100 ml absolute ethanol; 75 ml distilled water; 10 ml benzene; 10 ml ethyl acetate). The genital capsule was removed with fine forceps by gently squeezing the abdomen just anterior to the genital capsule. The capsule was placed in a porcelain crucible in a hot solution of 10% potassium hydroxide for clearing. The time necessary to achieve the desired clearing varied with different specimens; to ensure the proper degree of caustic action the capsule was removed to 70% ethanol every 4–5 minutes and checked under the microscope. The specimen was judged sufficiently clear when internal parts of the phallus could be seen through the capsule wall. After clearing, the capsule was transferred in order to the following solutions for three minutes each: glacial acetic acid, distilled water, distilled water (for a second rinse), and 70% ethanol.

The pygophore itself was dissected to study the morphology of the parameres and the sperm reservoir. First, the left clasper was removed using a bent-tipped needle mounted in a wooden matchstick to hook the inner projection. To obtain the sperm reservoir, the entire phallus, including the basal apparatus, was detached from the wall of the capsule and removed through the abdominal opening. The basal apparatus, phallosoma, and membranes were dissected away from the sperm reservoir in that order.

The clasper and sperm reservoir were each transferred in turn to a very small drop of glycerine for drawing. The left clasper of each specimen was drawn from an inner view, as if observing from the center of the capsule looking outward with the clasper *in situ.* In the Lethaeini this offers the best angle for viewing the clasper. Similar orientations were achieved by positioning the area of attachment with the aperture toward the viewer, and the shank as flat against the bottom of the spot plate as possible. Hairs have been omitted from most drawings, for the sake of clarity. The sperm reservoir was drawn in both lateral and dorsal views to convey maximum structural detail. Sclerotized areas are stippled and membranous regions of the bulb, where visible, have been represented by dashed lines.

Dissections were stored in numbered depressions in porcelain spot plates in glycerine. Each dissection was reassociated with the specimen from which it came by

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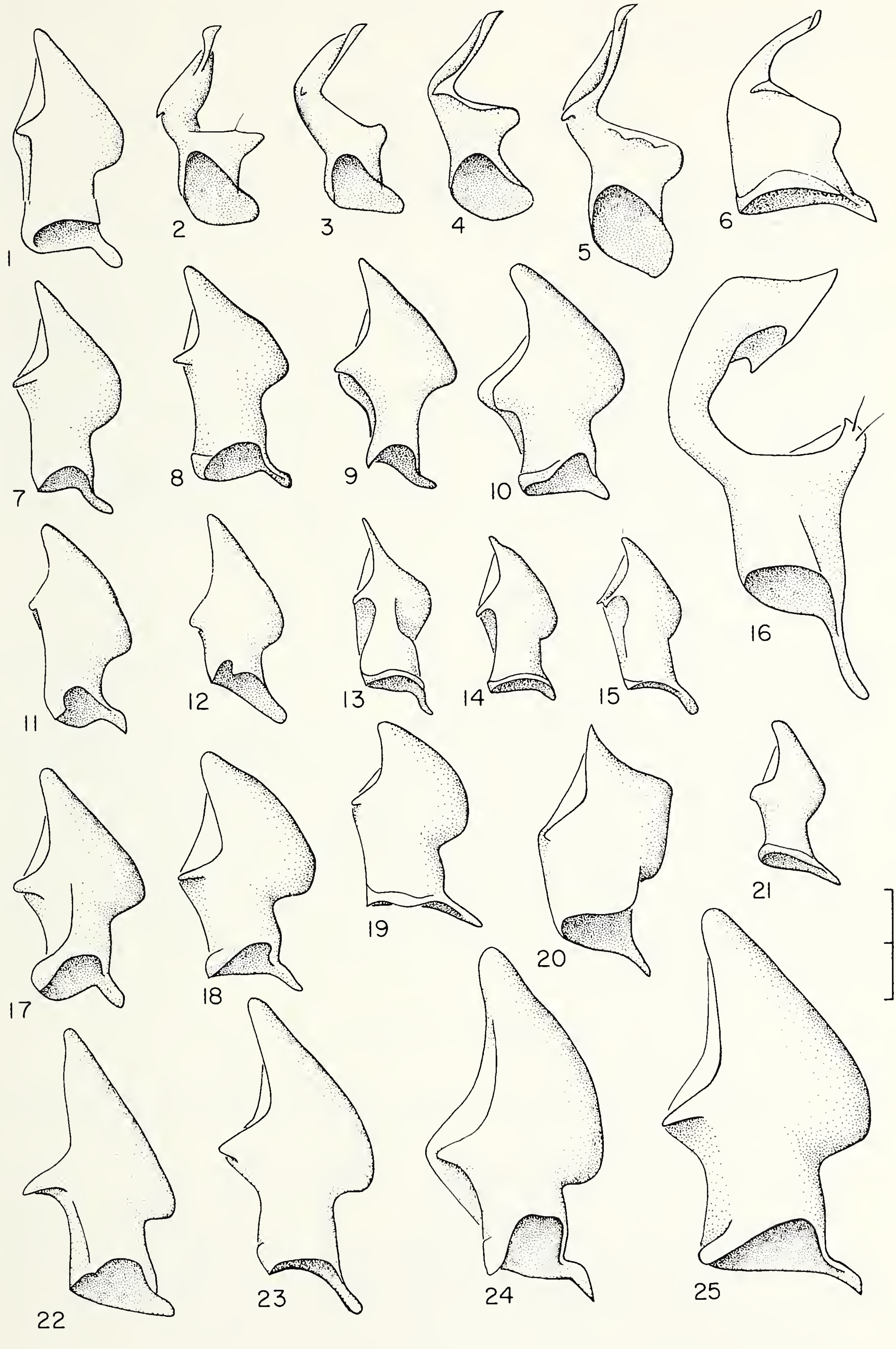
Figs. 1–25. Left paramere, inner view. Scale line = 0.1 mm. 1. *Cryphula trimaculata.* 2. *Paramyocara iridescens.* 3. *Paramyocara punctatum.* 4. *Exomyocara trispinosum.* 5. *Myocara* sp. 6. *Esuris terginus.* 7. *Cryphula affinis.* 8. *Cryphula fasciata.* 9. *Cryphula nitens.* 10. *Rhaptus quadricollis.* 11. *Bubaces* sp. 12. *Coleocoris ocellatus.* 13. *Lampropunctus hirsutus.* 14. *Lamproceps indicus.* 15. *Valtissius distinctus.* 16. *Hexatrichocoris melleus.* 17. *Paragonatas costaricensis.* 18. *Paragonatas divergens.* 19. *Xestocoris nitens.* 20. *Afromydrus slateri.* 21. *Lipostemmata* sp. 22. *Atkinsonianus reticulatus.* 23. *Gonatoides typicus.* 24. *Cistalia signoretti.* 25. *Petissius assimilandus.*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pinning a genitalia vial containing the dissected pieces in glycerine to the same pin as the dissected specimen.

RESULTS: GENITALIC DESCRIPTIONS

Adauctus Distant

Distribution: Oriental.

Species examined (1 of 1): *Adauctus cupreus* Distant: S. India Chikkaballapura, V. Campbell (JAS).

Clasper (Fig. 45): blade tapering to a relatively sharp, recurved point; shank short, twisted; area of attachment not prolonged laterally, without flange; inner projection prominent, acutely pointed, small mesal portion "spur-like"; outer projection broadly rounded, relatively flat.

Sperm reservoir (Figs. 116, 117): vesical seminal duct narrow; sleeve (not apparent) probably fused with vesical seminal duct; arcuate extension moderately sclerotized except around insertion of conjunctival seminal duct where it is heavily sclerotized; arcuate extension broadening distally in dorsal view; shape of membranous bulb unknown; wings and corrugations absent; holding sclerites (not shown in Fig. 117) long, thin, moderately sclerotized and converging distally.

Afromydrus Scudder

Distribution: Ethiopian.

Species examined (1 of 1): *Afromydrus slateri* (Southwood): Nigeria, Ikon CRIN, SE State, 4 April 1975, J. T. Medler (JAS).

Clasper (Fig. 20): blade tapering to a sharp point; shank broad; area of attachment without a flange; inner projection not strongly produced, broadly triangular, with small mesal portion; outer projection large, quadrate, with a rough texture.

Sperm reservoir (Figs. 136, 137): vesical seminal duct with a peculiar septum that divides the opening to the membranous bulb in half (not visible in Fig. 137); sleeve not apparent; arcuate extension ovoid in dorsal view, very flat in lateral view; membranous bulb double but lobes meeting at midline, giving the appearance of a single bulb; corrugations lacking; wings strap-like; holding sclerites moderately sclerotized, meeting distally to form a "v."

Aristaenetus Distant

Distribution: Australian.

Species examined (2 of 2): *Aristaenetus diffinis* (Walker) (type species): Australia,

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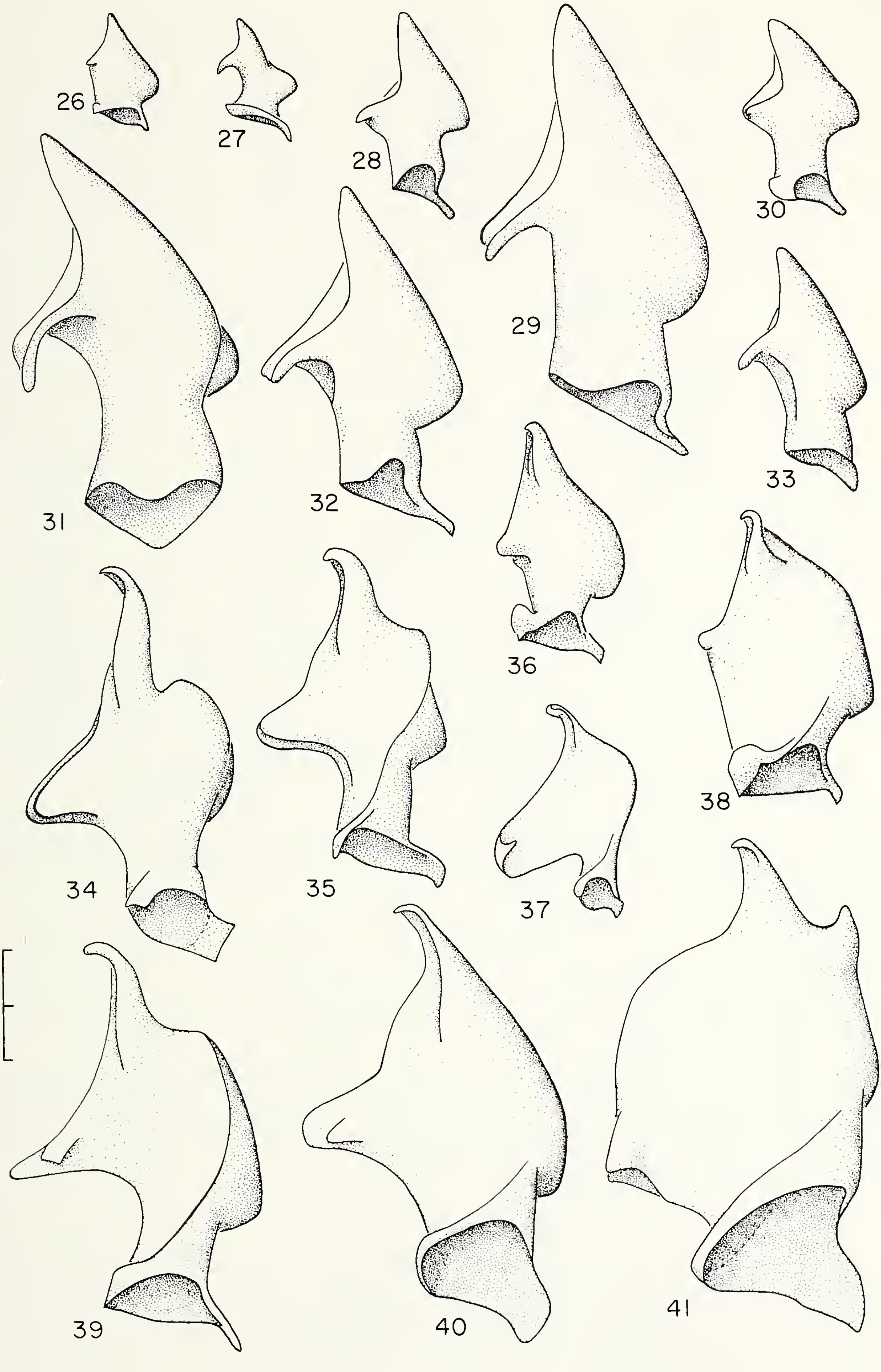
Figs. 26–41. Left paramere, inner view. Scale line = 0.1 mm except for Figs. 36–39 where it equals 0.25 mm. 26. *Ptilocamptocera franzi*. 27. *Camptocera glaberrima*. 28. *Sweetolethaeus macchiaensis*. 29. *Lethaeus longirostris*. 30. *Noteolethaeus armstrongi*. 31. *Lethaeus cribratissimus*. 32. *Lethaeus africanus*. 33. *Lethaeus nitidus*. 34. *Lophoraglius guttulatus*. 35. *Neolethaeus australiensis*. 36. *Neolethaeus aethiopicus*. 37. *Neolethaeus dallasi*. 38. *Neolethaeus giganteus*. 39. *Neolethaeus tenebrosus*. 40. *Aristaenetus diffinis*. 41. *Aristaenetus similis*.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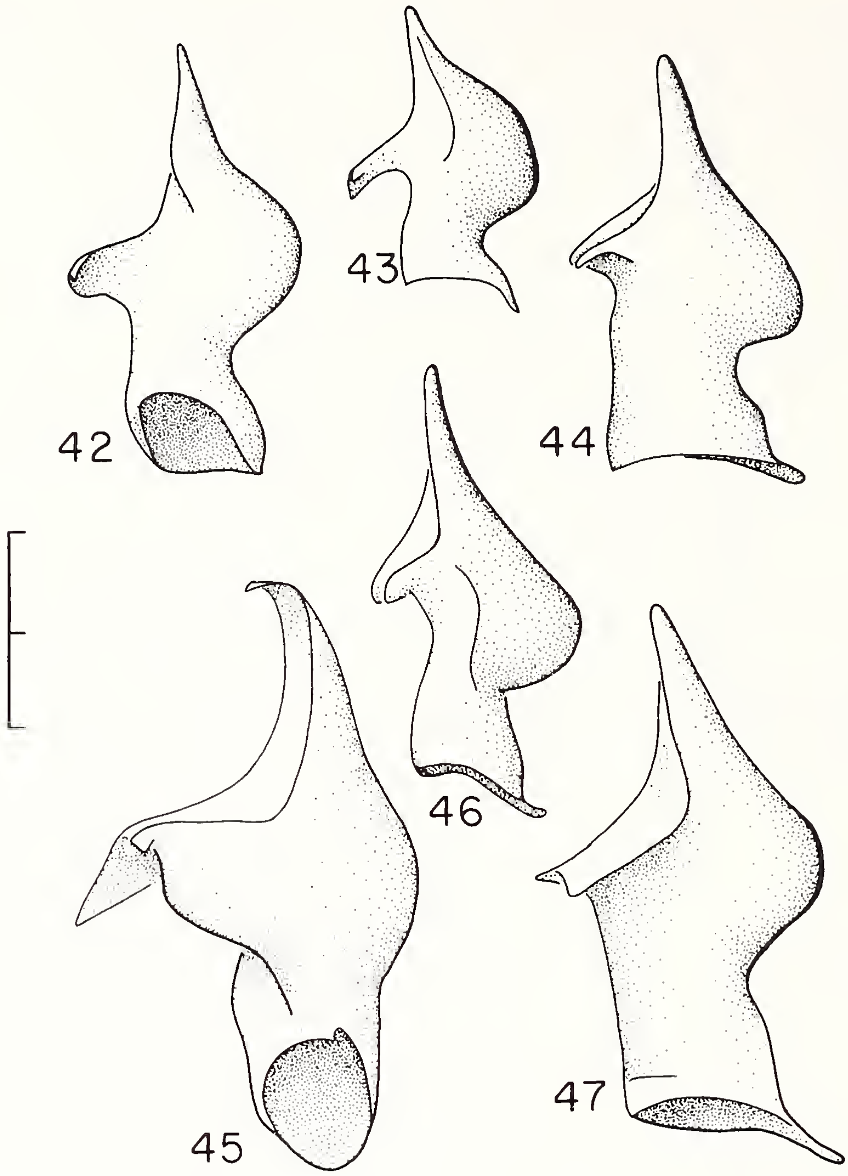

Figs. 42–47. Left paramere, inner view. Scale line = 0.1 mm. 42. *Diniella nitida.* 43. *Diniella laeviuscula.* 44. *Austroxestus australiensis.* 45. *Adauctus cupreus.* 46. *Diniella pallipes.* 47. *Diniella* sp.

Telegraph Xing, Dulhunty River, Cape York Pen., N. Qld., 2–4-vii-1975, G. B. Monteith (QSLD).

Aristaenetus similis Woodward and O'Donnell: Australia, Brisbane, Qld. 20-v-1964, H. A. Rose (QSLD).

Clasper (Figs. 40, 41): blade with apex narrow and curving, base of blade widened, to an extreme degree in *A. similis* (Fig. 41); shank reduced, concave where it meets the well-developed flange; inner and outer projections varying considerably in shape between species (compare Figs. 40, 41).

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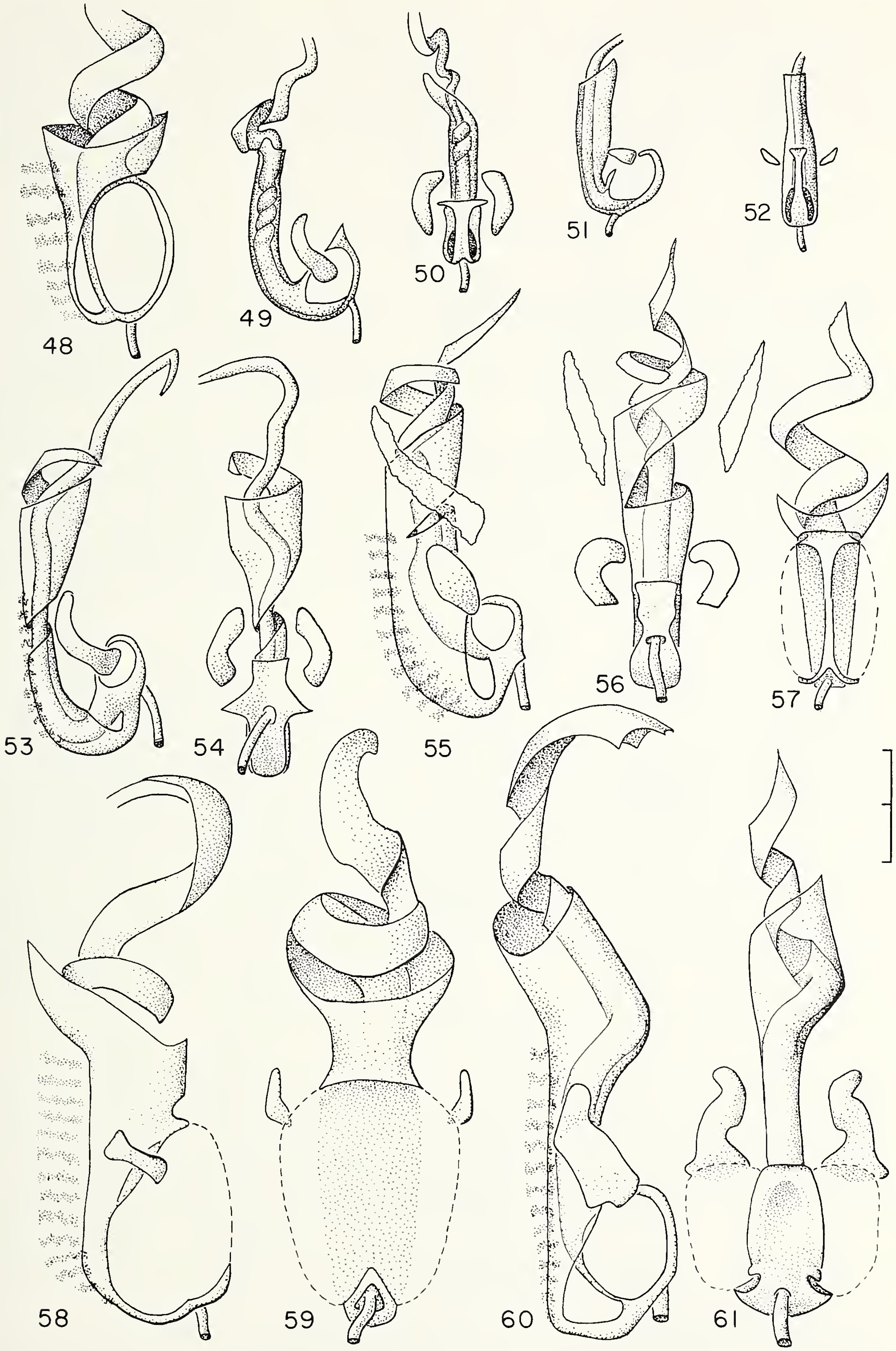
Figs. 48–61. Sperm reservoir, dorsal (d.v.) and lateral (l.v.) views. Scale line = 0.1 mm. 48. *Paragonatas divergens,* d.v. 49. *Coleocoris ocellatus,* l.v. 50. *Coleocoris ocellatus,* d.v. 51. *Esuris terginus,* l.v. 52. *Esuris terginus,* d.v. 53. *Paragonatas costaricensis,* l.v. 54. *Paragonatas costaricensis,* d.v. 55. *Gonatoides typicus,* l.v. 56. *Gonatoides typicus,* d.v. 57. *Paragonatas divergens,* d.v. 58. *Cistalia signoretii,* l.v. 59. *Cistalia signoretii,* d.v. 60. *Petissius assimilandus,* l.v. 61. *Petissius assimilandus,* d.v.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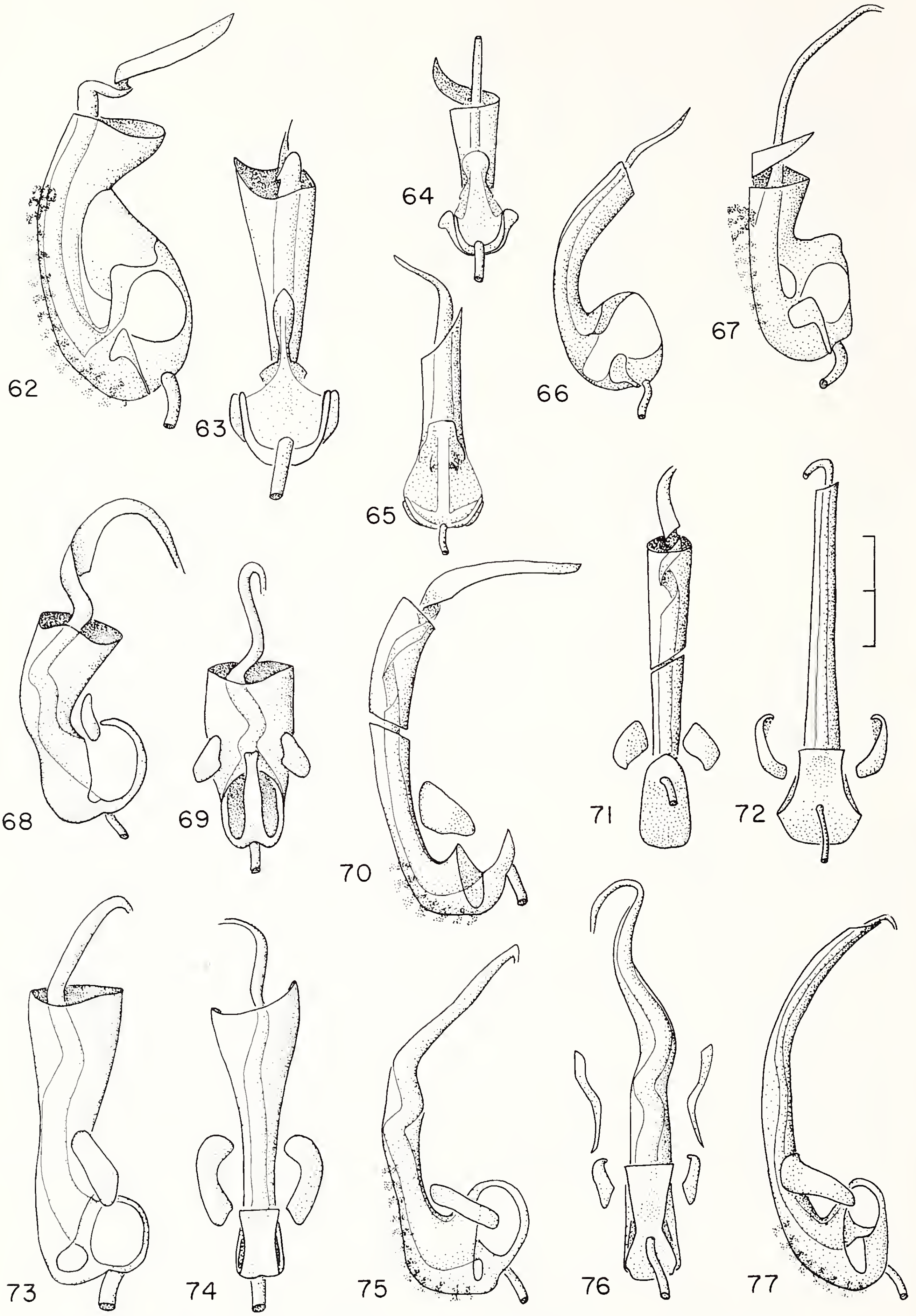

Figs. 62–77. Sperm reservoir, dorsal (d.v.) and lateral (l.v.) views. (Scale line = 0.1 mm.) 62. *Myocara* sp., l.v. 63. *Myocara* sp., d.v. 64. *Exomyocara trispinosum,* d.v. 65. *Paramyocara punctatum,* d.v. 66. *Paramyocara punctatum,* l.v. 67. *Exomyocara trispinosum,* l.v. 68. *Cryphula*

Sperm reservoir (Figs. 93, 94, 114, 118): vesical seminal duct long, coiled for several turns apically; sleeve moderately sclerotized, fused with vesical seminal duct distally; arcuate extension narrow or broad in dorsal view; shape of membranous bulb uncertain, probably single; wings short and broad; corrugations absent; holding sclerites very long, curving proximally around wings, and meeting distally to form a "v."

Atkinsonianus Distant

Distribution: Oriental.

Species examined (1 of 1): *Atkinsonianus reticulatus* Distant: N. India: Darjeeling 7,000 ft. 11-20-iii-1924, Maj. R. W. G. Hingston (BM).

Clasper (Fig. 22): blade long, apex pointed; area of attachment without a flange; inner projection narrow, pointed; outer projection with long blade portion, relatively acute.

Sperm Reservoir (Figs. 110, 111): vesical seminal duct twisted apically, and surrounded by moderately sclerotized sleeve; arcuate extension meeting an extension of the sleeve midway around the membranous bulb; membranous bulb double, each lobe slightly angled towards vesical seminal duct; wings quadrate; corrugations lacking; holding sclerites form a "v," but extremely faint and barely visible.

Austroxestus Woodward

Distribution: Australian.

Species examined (1 of 5): *Austroxestus australiensis* Woodward: Tasmania, Forth Falls via Sheffield, 5-II-1967, G. Monteith (QSLD).

Clasper (Fig. 44): blade narrow, tapering to a relatively sharp point; shank broad; area of attachment without a flange; inner projection prominent, with small, thin mesal portion; outer projection prominent, relatively acute.

Sperm Reservoir (Figs. 108, 109): Vesical seminal duct surrounded by a lightly sclerotized sleeve; sleeve and vesical seminal duct extending around "top" of membranous bulb to meet arcuate extension; arcuate extension rectangular in dorsal view; membranous bulb double, each lobe quite large (not illustrated); wings, corrugations, and holding sclerites absent.

Bubaces Distant

Distribution: Neotropical.

Species examined (1 of 4): *Bubaces uhleri* (Distant): St. Lucia, BWI, 2 mi N Castries, VI-22-1973, Baranowski, O'Rourke, Picchi, Slater (JAS).

Clasper (Fig. 11): blade considerably longer on outer curvature than on inner curvature; shank short; area of attachment without flange; inner projection small; outer projection relatively sharp.

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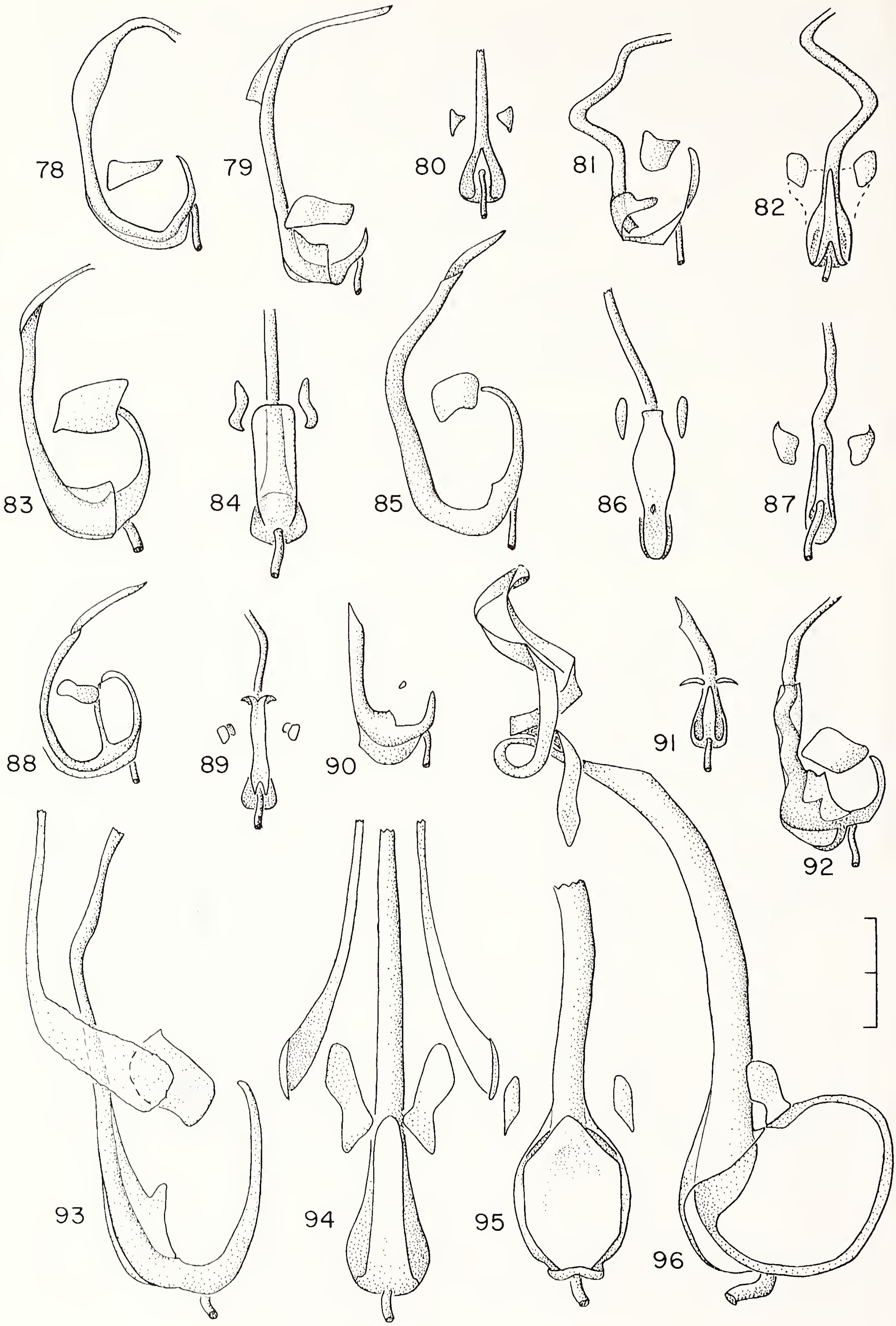
nitens, d.v. 69. *Cryphula nitens,* l.v. 70. *Cryphula affinis,* l.v. 71. *Cryphula affinis,* d.v. 72. *Cryphula fasciata,* d.v. 73. *Rhaptus quadricollis,* l.v. 74. *Rhaptus quadricollis,* d.v. 75. *Cryphula trimaculata,* l.v. 76. *Cryphula trimaculata,* d.v. 77. *Cryphula fasciata,* l.v.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Sperm Reservoir (Figs. 97, 98): vesical seminal duct surrounded by a proximally moderately sclerotized sleeve; sleeve with 2 "arms" that almost enclose conjunctival seminal duct, sleeve also with an extension opposite the arcuate extension; arcuate extension only lightly sclerotized; membranous bulb heart-shaped in dorsal view (not illustrated); wings rectangular, "bent" towards each other; corrugations and holding sclerites lacking.

Camptocera Jakovlev

Distribution: Palearctic, Ethiopian, Oriental.

Species examined (1 of 2); *Camptocera glaberrima* (Walker): Spain Madrid, IV-1909 (JAS).

Clasper (Fig. 27): blade small; shank wide, short; area of attachment with a flange; inner projection prominent, recurved apically; outer projection prominent, triangular, close to area of attachment.

Sperm Reservoir: (Figs. 90, 91): vesical seminal duct not surrounded by a sleeve; sleeve reduced to a heavily sclerotized structure just distal to insertion of conjunctival seminal duct; arcuate extension short, stout but tapering apically in dorsal view; wings narrow, thin, projecting out laterally instead of toward the vesical seminal duct; corrugations and holding sclerites absent.

Cistalia Stål

Distribution: Neotropical, Nearctic.

Species examined (2 of 5): *Cistalia micans* Slater and O'Donnell: Brazil Espiritu Santu: Linhares, Sept. 1972, M. Alvarenga (JAS) (see Slater and O'Donnell, 1978 for figures). *Cistalia signoretii* (Guerin-Meneville) (type species): Brazil Piracicaba S.P. XII-2-1965, C. A. Triplehorn, blacklight trap (JAS).

Clasper (Fig. 24): blade wide, prominent; shank reduced; area of attachment with partially developed flange; inner projection very large, triangular, with mesal portion quite large; outer projection large, meeting shank at a right angle near area of attachment.

Sperm Reservoir (Figs 58, 59): vesical seminal duct flattened and twisted apically; sleeve very prominent, widened distally; arcuate extension small; membranous bulb not bilobed; wings small, rectangular; corrugations heavily sclerotized, very prominent; holding sclerites absent.

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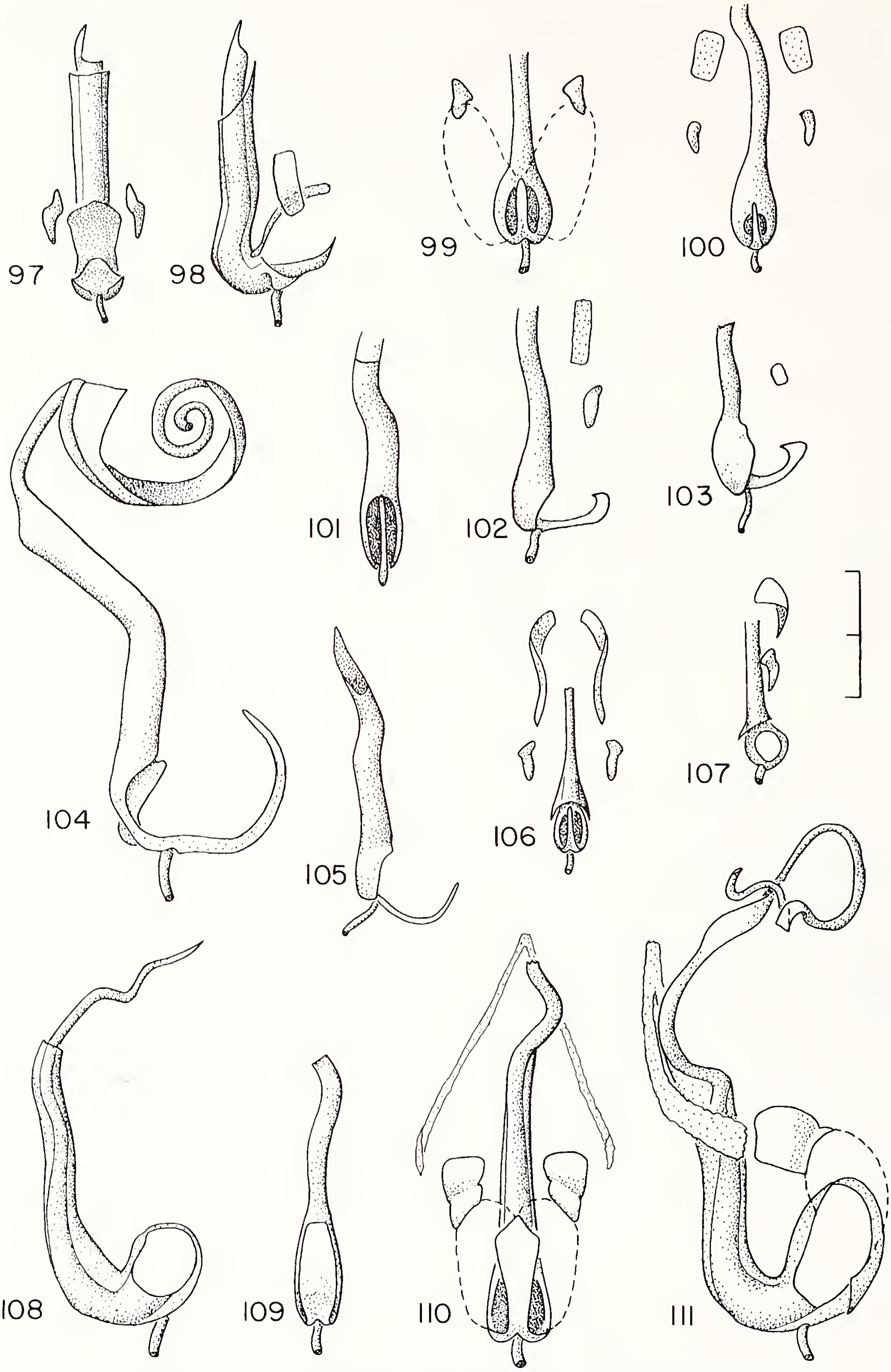
Figs. 78–96. Sperm reservoir, dorsal (d.v.) and lateral (l.v.) views. Scale line = 0.1 mm. 78. *Lipostemmata* sp., l.v. 79. *Lipostemmata major,* l.v. 80. *Lipostemmata* sp. (same as no. 78), d.v. 81. *Valtissius distinctus,* l.v. 82. *Valtissius distinctus,* d.v. 83. *Lamproceps indicus,* l.v. 84. *Lamproceps indicus,* d.v. 85. *Lampropunctus hirsutus,* l.v. 86. *Lampropunctus hirsutus,* d.v. 87. *Xestocoris nitens,* d.v. 88. *Ptilocamptocera franzi,* l.v. 89. *Ptilocamptocera franzi,* d.v. 90. *Camptocera glaberrima,* l.v. 91. *Camptocera glaberrima,* d.v. 92. *Xestocoris nitens,* d.v. 93. *Aristaenetus diffinis,* l.v. 94. *Aristaenetus diffinis,* d.v. 95. *Hexatrichocoris melleus,* d.v. 96. *Hexatrichocoris melleus,* l.v.



Figs. 97–111. Sperm reservoir, dorsal (d.v.) and lateral (l.v.) views. (Scale line = 0.1 mm.) 97. *Bubaces* sp., d.v. 98. *Bubaces* sp., l.v. 99. *Diniella laevicollis,* d.v. 100. *Diniella nitida,* l.v. 101. *Diniella pallipes,* d.v. 102. *Diniella nitida,* l.v. 103. *Diniella laevicollis,* l.v. 104. *Diniella* sp., l.v. 105. *Diniella pallipes,* l.v. 106. *Diniella laeviuscula,* d.v. 107. *Diniella laeviuscula,* l.v. 108. *Austroxestus australiensis,* l.v. 109. *Austroxestus australiensis,* d.v. 110. *Atkinsonianus reticulatus,* d.v. 111. *Atkinsonianus reticulatus,* l.v.

Coleocoris Gross

Distribution: Australian.

Species examined (1 of 3): *Coleocoris ocellatus* Gross: W. Australia Torbay 14 mi W Albany, XII-26-1971, J. A. Slater (JAS).

Clasper (Fig. 12): blade triangular, long and pointed; shank relatively short; area of attachment with a prominently "notched" aperture, lacking a flange; mesal portion of inner projection broad and thumb-like; outer projection broadly triangular.

Sperm Reservoir (Figs. 49, 50): vesical seminal duct tightly coiled within sleeve and twisted beyond it; sleeve forming a projection that extends almost to the arcuate extension; arcuate extension well-developed, with an apical protrusion visible in lateral view; membranous bulb with a lobe extending to each wing; wings rectangular; corrugations and holding sclerites lacking.

Cryphula Stål

Distribution: Neotropical, Nearctic.

Species examined (4 of 11): *Cryphula affinis* (Distant): Brazil Piracicaba, S.P., XI-11-1965, C. A. Triplehorn, black light (JAS).

Cryphula fasciata (Distant): Tole Panama Champion (JAS).

Cryphula nitens Barber: California Dune Lakes 3 mi S Oceano, X-11-1974, J. Doyen, stabilized dunes (JAS).

Cryphula trimaculata (Distant): Conn. Barn Island Stonington, VI-9-1976, Slater, O'Donnell, Ford (JAS).

Clasper (Figs. 1, 7, 8, 9): blade thickly pointed; flange present or absent; inner and outer projections at about same level along shank; clasper divided almost equally into shank and blade.

Sperm Reservoir (Figs. 68–72, 75–77): vesical seminal duct bent and/or twisted; sleeve prominent, narrow (except in *C. nitens,* Figs. 68, 69); arcuate extension small (Fig. 70), or forming an incomplete bridge (Fig. 68) or complete bridge (Figs. 75, 77) around membranous bulb; membranous bulb double; wings broad (Figs. 70, 71) or relatively long and slender; corrugations present or absent; holding sclerites present or absent.

Diniella Bergroth

Distribution: Ethiopian, Oriental, Australian.

Species examined (5 of 17): *Diniella laevicollis* (Reuter): S. Africa Kruger Nat. Park, 3 mi. E. Satara Camp, 29 Apr. 68, Nwanedzi River J. A. and S. Slater, M. Sweet, T. Schuh (JAS).

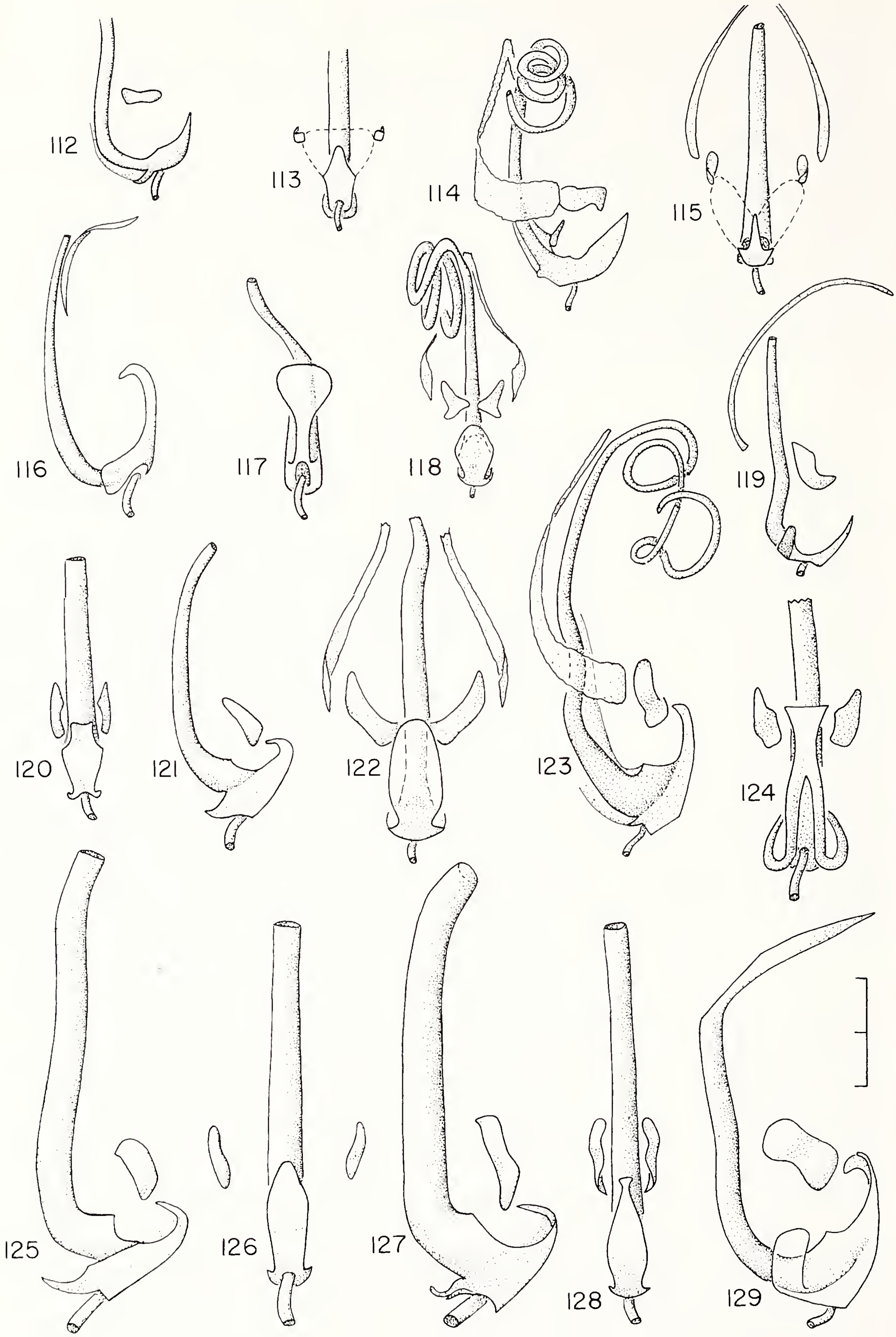
Diniella laeviuscula (Bergroth): Philippines, Luzon, IRRI farm, April 19, 1972, A. D. Pawar (JAS).

Diniella nitida (Reuter): S. Africa Natal Lake, St. Lucia, Charters Creek, Nov. 12, 1967, J. A. and S. Slater, T. Schuh (JAS).

Diniella pallipes (Scott): Shika Is., Fukuoka, X-21-1954, T. Hidaka (JAS).

Diniella sp.: Congo Belge, P.N.U. Kaziba affl. g. Senze S. affl. dr. Lufira (1.140 m.) 4-12-II-1948, Mis G. F. deWitte 1266a (JAS).

Clasper (Figs. 42, 43, 46, 47) (*D. laevicollis* not illustrated): blade slender, tapering to a relatively sharp point; shank broad or slender; area of attachment without a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flange; inner projection variable; outer projection broadly rounded (Figs. 42, 43) or relatively more acute (Fig. 46).

Sperm Reservoir (Figs. 99–107) (*Diniella* sp. not shown in d.v.): vesical seminal duct with sleeve apparent only in *D. laeviuscula* (Figs. 106, 107) and *D.* sp. (Fig. 104); vesical seminal duct otherwise partially or completely fused with sleeve; arcuate extension long, thin in both dorsal and lateral views, curved or straight at apex, and forming a complete bridge in one species, *D. laeviuscula* (Fig. 107); membranous bulb double, lobes large; wings usually small, absent in *D. pallipes*; corrugations lacking; holding sclerites absent (Figs. 101, 105), or lightly sclerotized and of various configurations.

Esuris Stål

Distribution: Neotropical.

Species examined (1 of 1): *Esuris terginus* (Stål): Brazil Nova Teutonia, Santa Catarina 27°11′N, 52°23′W, July 10, 1960, Fritz Plaumann (JAS).

Clasper (Fig. 6): highly modified; blade narrow, arising on the inner side of the clasper and extending laterally in the opposite direction from the usual case; base of blade with a small projection pointing mesally (actually the inner projection); shank broad, somewhat flattened; area of attachment with a flange; outer curvature deeply concave; outer projection a small blunt protrusion.

Sperm Reservoir (Figs. 51, 52): vesical seminal duct surrounded by a moderately sclerotized sleeve; arcuate extension well developed, heavily sclerotized; membranous bulb presumably double; wings rectangular; corrugations and holding sclerites lacking.

Exomyocara Slater and Woodward

Distribution: Australian.

Species examined (1 of 2): *Exomyocara tripinosum* Slater and Woodward (type species): Wildlife reserve 21 mi N Perth, W. Australia, XII-16-1971, J. A. Slater, paratype (JAS).

Clasper (Fig. 4): highly modified, "reversed"; inner projection sharply curved toward outer aspect of clasper, with flared ridge along inner angle; outer projection thumb-like.

Sperm Reservoir (Figs. 64, 67): vesical seminal duct surrounded by a prominent sleeve; sleeve with a "lip" near insertion of vesical seminal duct, and also with a

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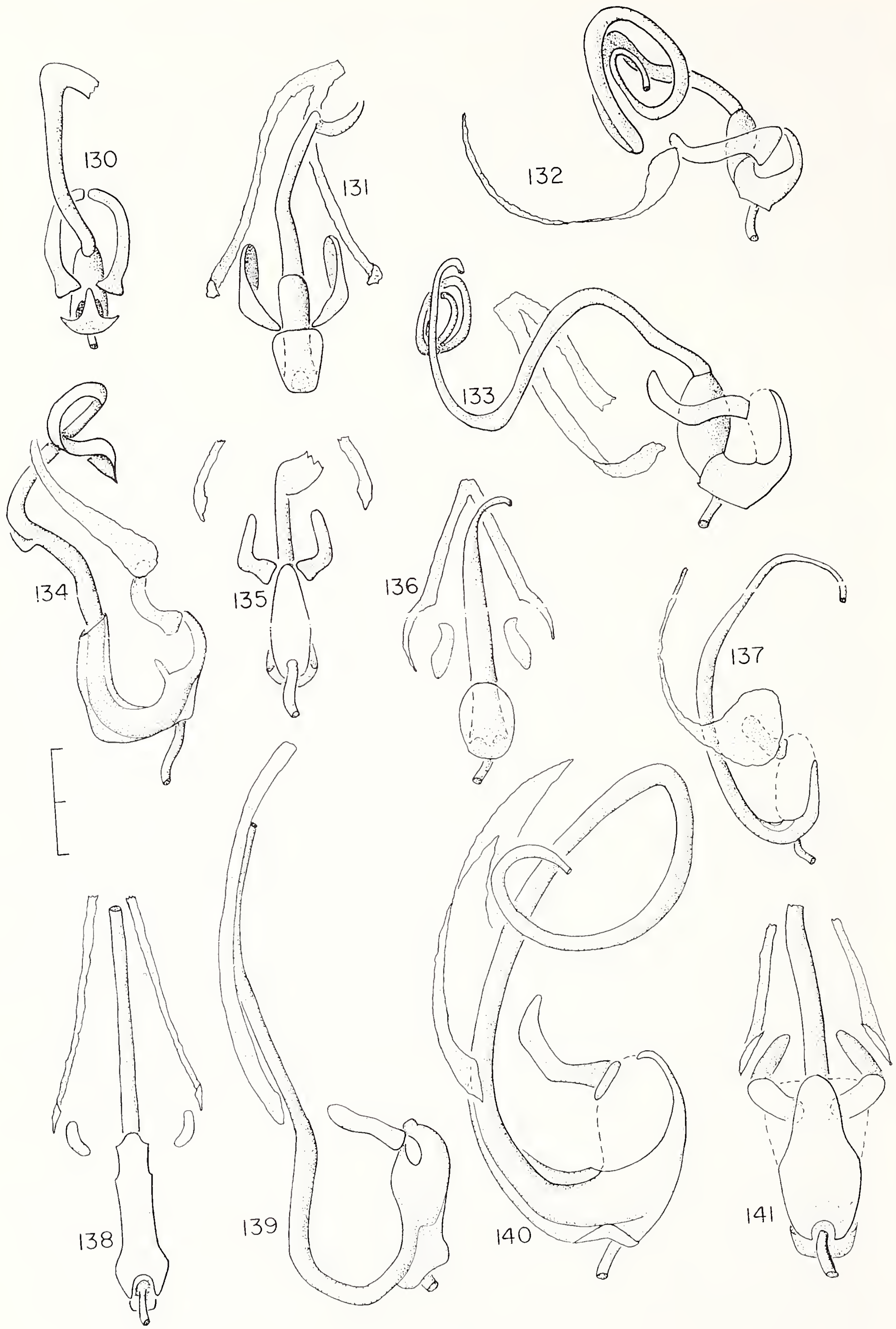
Figs. 112–129. Sperm reservoir, dorsal (d.v.) and lateral (l.v.) views. Scale line = 0.1 mm except for figures 114 and 118 where it = 0.25 mm. 112. *Noteolethaeus armstrongi,* l.v. 113. *Noteolethaeus armstrongi,* d.v. 114. *Aristaenetus similis,* l.v. 115. *Sweetolethaeus macchiaensis,* d.v. 116. *Adauctus cupreus,* l.v. 117. *Adauctus cupreus,* d.v. 118. *Aristaenetus similis,* d.v. 119. *Sweetolethaeus macchiaensis,* l.v. 120. *Lethaeus nitidus,* d.v. 121. *Lethaeus nitidus,* l.v. 122. *Lophoraglius guttulatus,* d.v. 123. *Lophoraglius guttulatus,* l.v. 124. *Lethaeus africanus,* d.v. 125. *Lethaeus longirostris,* l.v. 126. *Lethaeus longirostris,* d.v. 127. *Lethaeus cribratissimus,* l.v. 128. *Lethaeus cribratissimus,* d.v. 129. *Lethaeus africanus,* l.v.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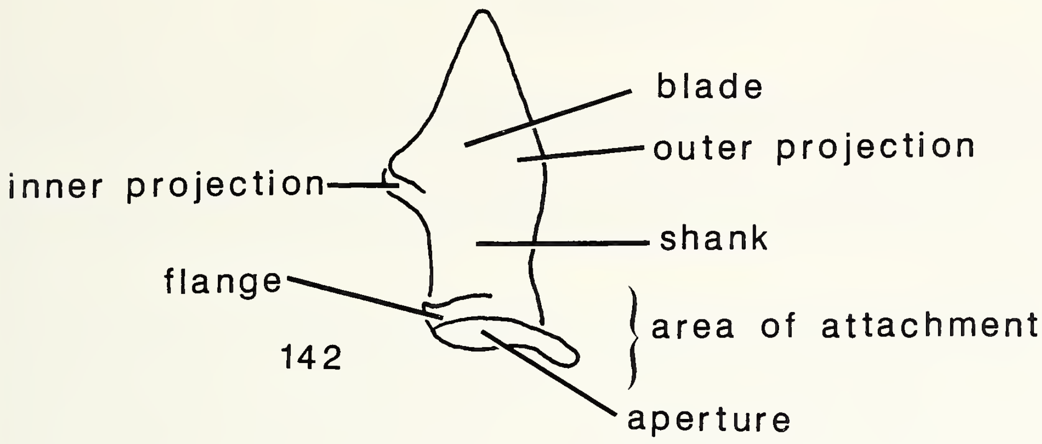

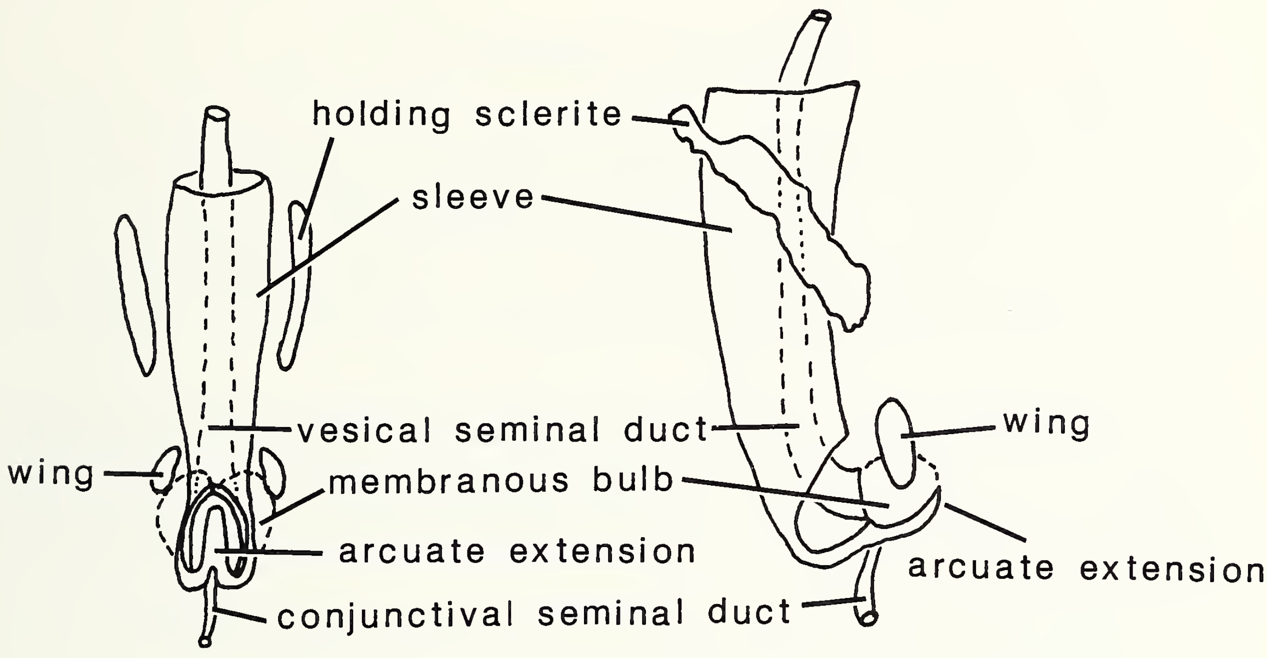

Figs. 142–144. 142. Diagrammatic lethaeine clasper, inner view.143,144. Diagrammatic generalized lethaeine sperm reservoir. 143. Lateral view. 144. Dorsal view.

heavily sclerotized projection dorsally that joins arcuate extension; sleeve ending in an apical twist, arcuate extension only lightly sclerotized; shape of membranous bulb uncertain (presumably similar to *Myocara*); wings and holding sclerites absent; corrugations prominent, especially the distal triangular patch.

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Figs. 130–141. Sperm reservoir, dorsal (d.v.) and lateral (l.v.) views. Scale line = 0.1 mm except for Figs. 130–133 where it = 0.25 mm. 130. *Neolethaeus aethiopicus*, d.v. 131. *Neolethaeus giganteus*, d.v. 132. *Neolethaeus aethiopicus*, l.v. 133. *Neolethaeus giganteus*, l.v. 134. *Neolethaeus australiensis*, l.v. 135. *Neolethaeus australiensis*, d.v. 136. *Afromydrus slateri*, d.v. 137. *Afromydrus slateri*, l.v. 138. *Neolethaeus tenebrosus*, d.v. 139. *Neolethaeus tenebrosus*, l.v. 140. *Neolethaeus dallasi*, d.v. 141. *Neolethaeus dallasi*, l.v.

Gonatoides Slater

Distribution: Neotropical.

Species examined (1 of 1): *Gonatoides typicus* (Distant): Trinidad: 3 mi E Arima, VI-15-1973, R. Baranowski, F. O'Rourke, V. Picchi, J. Slater (JAS).

Clasper (Fig. 23): Shank broad, tapering to a subacute tip; shank narrower than blade; area of attachment with small partial flange on inner aspect; inner and outer projections prominent.

Sperm Reservoir (Figs. 55, 56): vesical seminal duct twisted and apically "flattened"; sleeve heavily sclerotized, distinct, and helicoid distally; arcuate extension prominent, broad in dorsal view and forming a complete bridge; membranous bulb double, each lobe relatively small; wings thick, curving; corrugations prominent; holding sclerites relatively long, diverging distally.

Hexatrichocoris Kiritshenko

Distribution: Oriental.

Species examined (1 of 1): *Hexatrichocoris melleus* Kiritshenko: Sikkim Tautang 6,000′, IV-24-1924, Maj. R. W. G. Hingston (paratype) (JAS).

Clasper (Fig. 16): highly modified; blade "c-shaped" and extremely large, arising on the mesal side of the clasper and curving outward; apex of blade flattened into a plate (not visible in figure); shank broad, folded longitudinally; area of attachment without a flange; outer projection prominent, thumb-like.

Sperm Reservoir (Figs. 95, 96): vesical seminal duct fused with sleeve except proximally (near insertion of conjunctival seminal duct and where arcuate extension meets the sleeve); vesical seminal duct becoming a "twisted ribbon" apically; arcuate extension wide in dorsal view; membranous bulb double; wings relatively small; corrugations and holding sclerites lacking. The phallus of *Hexatrichocoris melleus* is unusual in the Lethaeini in that 4 (2 pair) large sclerotized spines are present on what I assume to be the conjunctiva (not illustrated). It is unfortunate that their position on the inflated phallus could not be determined.

Lamproceps Reuter

Distribution: Ethiopian, Oriental.

Species examined (1 of 6): *Lamproceps indicus* (Dallas) (type species): Nigeria Lokoja, Kabba, II-24-1949, B. Malkin (JAS).

Clasper (Fig. 14): blade wide, tapering to a sharp point; shank flaring slightly towards base; area of attachment with flange; inner projection triangular, mesal portion small, narrow; outer projection relatively flat.

Sperm Reservoir (Figs. 83, 84): vesical seminal duct twisted apically; sleeve moderately sclerotized, apparent only proximally around vesical seminal duct; arcuate extension long, rectangular in dorsal view; membranous bulb presumably not bilobed; wings quadrate in lateral view; faint corrugations present (not shown in Fig. 83); holding sclerites lacking.

Lampropunctus Scudder

Distribution: Ethiopian.

Species examined (1 of 1): *Lampropunctus hirsutus* Scudder: S. Africa, Transvaal

Zoutpansberg 4,500′, 5 mi N Louis Trichardt, May 6, 1968, J. A. and S. Slater, M. Sweet, and T. Schuh (JAS).

Clasper (Fig. 13): blade narrow, pointed apically; shank "folded"; area of attachment with flange; inner projection triangular, with mesal portion finger-like and not produced extensively; outer curvature with extremely long hairs (not illustrated) on blade portion extending well beyond blade apex; outer projection relatively sharply rounded.

Sperm Reservoir (Figs. 85, 86): vesical seminal duct not surrounded by a sleeve; sleeve fused with vesical seminal duct or lost completely through reduction; arcuate extension long, bulging broadly in dorsal view; membranous bulb appearing bilobed in dorsal view, with each lobe extending to a wing; wings quadrate in lateral view; corrugations and holding sclerites lacking.

Lethaeus Dallas

Distribution: Ethiopian, Palearctic, Oriental.

Species examined (4 of 31): *Lethaeus africanus* Dallas (type species): Nigeria Lokoja Kabba, II-24-49, B. Malkin (JAS).

Lethaeus cribratissimus Stål: Cyprus Polemedia Hills, 600′, II-7-1950, G. Mavrormoustakis (JAS).

Lethaeus longirostris Reuter: Africa: Kenya: Nairobi, K. C., 12-IX-1953, D. C. Thomas (JAS).

Lethaeus nitidus Douglas and Scott: "Cephal Walker," (Greece) (JAS).

Clasper (Figs. 29, 31–33): blade long, tapering to a relatively sharp tip; shank broad, relatively short; area of attachment with lateral extension (except in *Lethaeus cribratissimus,* Fig. 31); inner projection long, finger-like; outer projection only moderately produced.

Sperm Reservoir (Figs. 120, 121, 124–129): vesical seminal duct broad; sleeve apparently reduced to a small spur near insertion of conjunctival seminal duct; conjunctival seminal duct broad in diameter; membranous bulb double, one lobe extending to each wing; wings variable in shape; corrugations and holding sclerites lacking.

Lipostemmata Berg

Distribution: Neotropical.

Species examined (2 of 3): *Lipostemmata major* Ashlock: Paraguay Central Ascuncion, verano, B. Podtiaguin (JAS).

Lipostemmata sp.: Paraguay Central Ascuncion, verano, B. Podtiaguin (JAS).

Clasper (Fig. 21) (*Lipostemmata major* not illustrated): blade relatively wide, tapering apically; shank conventional in illustrated species but expanded just basal to inner projection in *L. major*; area of attachment extending laterally beyond level of of outer projection, with flange; inner projection blunt (Fig. 21) or pointed (not shown); outer projection relatively small.

Sperm Reservoir (Figs. 78–80) (*L. major* not illustrated in d.v.): vesical seminal duct with expanded portion midway to apex; sleeve reduced, fusing with vesical seminal duct distally; arcuate extension short and curving; membranous bulb egg-

shaped, apparently not bilobed; wings rectangular; corrugations and holding sclerites absent.

Lophoraglius Wagner

Distribution: Ethiopian.

Species examined (1 of 8): *L. guttulatus* (Stål): S. Africa Umtentwenti, Natal, VII-1950, A. L. Capener (JAS).

Clasper (Fig. 34): blade relatively slender, pointed, and curving apically; shank narrow; area of attachment with a partial flange, lateral prolongation wide; inner projection large, with large mesal portion; outer projection broadly convex.

Sperm Reservoir (Figs. 122, 123); vesical seminal duct long, coiled distally; sleeve lightly sclerotized, reduced; arcuate extension ovoid in dorsal view; membranous bulb small apparently not double; wings rectangular; corrugations lacking; holding sclerites long, curving towards wings, and meeting distally in a distinct "v."

Myocara Bergroth

Distribution: Australian.

Species examined (1 of 2): *Myocara* sp.: Australia, Parra Wirra Nt. Park near Adelaide, S. Australia, I-5-1972, J. A. Slater (JAS).

Clasper (Fig. 5): highly modified, "reversed"; blade narrow, arising on inner side of clasper, extending laterally towards outer curvature; apex of blade sharply pointed; shank reduced on inner aspect; outer projection blunt, thumb-like, with shelf-like ridge; area of attachment slightly produced laterally, with large aperture and no flange.

Sperm Reservoir (Figs. 62, 63): vesical seminal duct twisted apically, surrounded by a heavily sclerotized sleeve; sleeve with a "lip" near insertion of conjunctival seminal duct; dorsal aspect of sleeve very heavily sclerotized with a projection at the arcuate extension; arcuate extension lightly sclerotized, more visible in lateral view; membranous bulb double, large and quite complex; each lobe extending to the distal end of the sleeve; wings absent, perhaps having fused to form the heavily sclerotized area on the dorsal aspect of the sleeve; holding sclerites absent; corrugations very prominent, with a thickened triangular patch distally.

Neolethaeus Distant

Distribution: Ethiopian, Australian, Oriental.

Species examined (5 of 20): *Neolethaeus aethiopicus* Hesse: Tanzania, Ilonga, IV-14-1965, I. A. D. Robertson, light trap (JAS).

Neolethaeus australiensis Woodward: Australia, McArthur River, N.T. 1-VI-1967, J. Sawdy (JAS).

Neolethaeus dallasi (Scott), Japan Mt. Rokko nr. Kobe, IX-6-1952, E. Nakanishi (JAS).

Neolethaeus giganteus Scudder, Nigeria U-I Campus 1-11-1971, under leaves, Albert V. Oboite (JAS).

Neolethaeus tenebrosus (Distant): Australia Mossman Gorge via Mossman, N. Qld., 25-26-XII-1964, H. A. Rose (JAS).

Clasper (Figs. 35–39): blade slender or broad, but always with curving apex; shank

reduced, often modified by an enlarged flange extending from area of attachment; inner projection varying from relatively small (Figs. 36, 38) to enormously enlarged (Fig. 37) or double (Fig. 39); outer projection prominent, rounded or truncate.

Sperm Reservoir (Figs. 130–135, 138–141), vesical seminal duct long, usually with several apical coils; sleeve apparent (Fig. 134, 140), or partially fused with vesical seminal duct to form a thickened region just distal to opening of vesical seminal duct (Figs. 132, 133) or fused entirely with vesical seminal duct (Fig. 139); arcuate extension varying in dorsal view from small and triangular (Fig. 130) to broad and sub-quadrate (Fig. 131); membranous bulb double, with a tendency to "unite," since lobes are usually quite small; wings long, curving towards vesical seminal duct; corrugations lacking; holding sclerites faint, not forming a "v" (Figs. 134, 135), or prominent, heavily sclerotized and appearing "v-shaped." The considerable variation present in this genus is explored in the Discussion.

Noteolethaeus Woodward and Slater

Distribution: Australian, Ethiopian.

Species examined (1 of 2): *Noteolethaeus armstrongi* Woodward and Slater (type species): Australia, Mt. Coot-tha, Brisbane, Qld., Aug. 9, 1966, R. A. Crowson ex litter (QSLD).

Clasper (Fig. 30): blade triangular, apex bluntly rounded; shank conventional; area of attachment with a wide flange and small aperture; inner projection large, triangular, with small mesal portion; outer projection sharply rounded, meeting blade portion at nearly a right angle.

Sperm Reservoir (Figs. 112, 113): vesical seminal duct heavily sclerotized; sleeve very faint, apparent only ventrally, with a spur present near insertion of conjunctival seminal duct; arcuate extension broad basally, tapering distally, in dorsal view; membranous bulb heart-shaped in dorsal view; wings rectangular, curving toward vesical seminal duct; corrugations and holding sclerites absent.

Paragonatas Barber

Distribution: Neotropical.

Species examined (2 of 2): *Paragonatas costaricensis* (Distant): Panama Maje Station, 90°09'N, 78°47'W, V-17-1975, Engleman, Ramirez, light (JAS).

Paragonatas divergens (Distant) (type species): Dominica 1.5 mi W Rasade, 22-VI-1971, Slater, Baranowski, Harrington (JAS).

Clasper (Figs. 17, 18): blade stout, tapering to a blunt point; shank conventional; area of attachment with an incomplete flange; mesal portion of inner projection short and broad (Fig. 17) or longer and more slender (Fig. 18); outer projection large, prominent.

Sperm Reservoir (Figs. 48, 53, 54, 57): The sperm reservoirs of these two species are quite different and are described separately. See Discussion for further comments.

P. costaricensis (Figs. 53, 54): vesical seminal duct surrounded by a heavily sclerotized, markedly helicoid sleeve; arcuate extension flaring and forming a wide "bridge" across membranous bulb; membranous bulb with 2 small lobes; wings long and slender, very heavily sclerotized; corrugations prominent; holding sclerites lacking.

P. divergens (Figs. 48, 57): vesical seminal duct large in diameter, changing from

a tube to an open "half-tube" as it emerges from the sleeve; sleeve well-developed but short, flaring distally to form a wide opening; arcuate extension narrow and strap-like, continuous with vesical seminal duct; membranous bulb bilobed but lobes not extending laterally; corrugations prominent; wings and holding sclerites lacking.

Paramyocara Woodward and Malipatil

Distribution: Australian, New Zealand.

Species examined (2 of 2): *Paramyocara iridescens* Woodward and Malipatil (type species): Australia, Mt. Carbine, N. Qld., 5-I-1964, G. Montieth (QSLD).

Paramyocara punctatum Woodward and Malipatil: Australia, Brisbane Qld., 22-IV-1969, G. Montieth (QSLD).

Clasper (Figs. 2, 3): highly modified, "reversed" as in *Exomyocara* and *Myocara* (see above); inner projection with hooked apex and small projection at base.

Sperm Reservoir (Figs. 65, 66): vesical seminal duct surrounded by a sleeve; sleeve lipped near insertion of conjunctival seminal duct; dorsal projection of sleeve moderately sclerotized; arcuate extension narrow, very lightly sclerotized, not meeting projection of sleeve; membranous bulb appearing single (a division at midline is visible only when closely examined), not extending much beyond sleeve; wings (contrary to Woodward and Malipatil, 1977) and holding sclerites lacking; corrugations extremely faint, without prominent triangular patch distally.

The sperm reservoir of the type species, *P. iridescens,* is so similar to *Exomyocara trispinosum* that it is not illustrated (see Discussion).

Petissius Distant

Distribution: Neotropical.

Species examined (1 of 3): *Petissius assimilandus* Distant (type species): Panama Las Cumbres, 09°06′N, 79°32′W, XI-13-1973, H. Wolda, light trap (JAS).

Clasper (Fig. 25): broadly triangular; blade tapering to a blunt tip; shank not as large as blade; outer projection prominent; inner projection with small finger-like mesal portion; area of attachment with lateral extension and partial flange.

Sperm Reservoir (Figs. 60, 61): vesical seminal duct large in diameter, with a large bend within the sleeve and two twists beyond it; sclerotized portion of vesical seminal duct ending in two prongs; sleeve strongly sclerotized, close to vesical seminal duct at least proximally, widening distally; arcuate extension forming a continuous bridge; membranous bulb double, each lobe relatively large but not extending beyond bridge of arcuate extension; wings heavily sclerotized, flared where they touch lobes of the bulb; corrugations present but not prominent; holding sclerites lacking.

Ptilocamptocera Wagner

Distribution: Ethiopian.

Species examined (1 of 2): *Ptilocamptocera franzi* Wagner (type species): Nigeria Lokoja Kabba, II-24-1949, B. Malkin (JAS).

Clasper (Fig. 26): blade triangular, tapering to a pointed tip; shank reduced on outer aspect due to large outer projection; area of attachment with incomplete flange;

inner projection triangular with small mesal portion; outer projection relatively acute, joining shank nearly at area of attachment.

Sperm Reservoir (Figs. 88, 89): vesical seminal duct with a prominent twist; sleeve visible ventrally along vesical seminal duct; arcuate extension curving around membranous bulb to meet a projection of the vesical seminal duct; membranous bulb bilobed; wings rectangular; corrugations and holding sclerites lacking.

Rhaptus Stål

Distribution: Neotropical.

Species examined (1 of 1): *Rhaptus quadricollis* (Spinola): Chile Renca Prov. Santiago, VI-1953, L. E. Pena (JAS).

Clasper (Fig. 10): blade broad; shank relatively narrow; area of attachment with flange; inner projection large, bluntly rounded, with mesal portion large and thumblike; outer projection large, broadly rounded.

Sperm Reservoir (Figs. 73, 74): vesical seminal duct loosely coiled, surrounded by a wide, heavily sclerotized sleeve; conjunctival seminal duct large in diameter; arcuate extension forming a complete bridge; membranous bulb double; wings rectangular, curving towards sleeve; corrugations and holding sclerites absent.

Sweetolethaeus Slater

Distribution: Ethiopian.

Species examined (1 of 2): *Sweetolethaeus macchiaensis* Slater (type species): S. Africa Capetown C.P. Signal Hill, 2,000′, X-5-1974, S. Slater, J. Ecker (JAS).

Clasper (Fig. 28): blade prominent, triangular, apex broadly pointed; shank smaller than blade portion; area of attachment without a flange; inner projection broad, with prominent, finger-like mesal portion; outer projection relatively acute, joining shank at the same level as inner projection.

Sperm Reservoir (Figs. 115, 119): vesical seminal duct not enclosed by a sleeve; sleeve apparently reduced to a thickened "ring" surrounding the opening of the vesical seminal duct; arcuate extension slender; membranous bulb double, lobes large; wings narrow, curving distally; corrugations absent; holding sclerites long, very lightly sclerotized, meeting to form a distinct "v" (distal junction of sclerites not shown in Fig. 115).

Valtissius Barber

Distribution: Nearctic, Neotropical.

Species examined (1 of 3): *Valtissius distinctus* (Distant): Grenada BWI St. George Parish, St. Pauls, VI-18-1973, Baranowski, O'Rourke, Picchi, Slater (JAS).

Clasper (Fig. 15): blade wide, tapering to an acute point; shank extensive; area of attachment with flange; inner projection very broad, produced about as much as broadly rounded outer projection, with small triangular mesal portion.

Sperm Reservoir (Figs. 81, 82): vesical seminal duct with 3 assymetrical twists; sleeve moderately sclerotized, apparent only near opening of vesical seminal duct; arcuate extension long and narrow in dorsal view; membranous bulb bilobed; wings quadrate; corrugations and holding sclerites lacking.

Xestocoris Van Duzee

Distribution: Nearctic, Neotropical.

Species examined (1 of 2): *Xestocoris nitens* Van Duzee: Conn. Mansfield Center, IV-19-1956, J. A. Slater (JAS).

Clasper (Fig. 19): blade very wide, tapering to a blunt point; shank broad; area of attachment with flange; inner projection triangular but not strongly produced, mesal portion small, finger-like; outer projection large, broadly and convexly rounded.

Sperm Reservoir (Figs. 87, 92): vesical seminal duct with several bends; sleeve lightly sclerotized proximally except for a "spur" near insertion of conjunctival seminal duct, moderately sclerotized distally where it is tightly appressed to the seminal duct; arcuate extension long and slender in dorsal view; membranous bulb double, each lobe extending to a wing; wings quadrate; corrugations and holding sclerites absent.

DISCUSSION

Lethaeine sperm reservoirs, and to a lesser degree claspers, exhibit a wide variety of form. While many genera exhibit a characteristic sperm reservoir morphology, several genera are so variable that their monophyly is in question. Obviously, more species and type species, and other characters, need to be examined before formal taxonomic changes at the generic level are proposed. It is clear, however, that both the clasper and sperm reservoir offer great potential not only for distinguishing among species, but also for grouping species into monophyletic genera and for combining genera into related groups.

The clasper is relatively less complex than the sperm reservoir, and is less informative phylogenetically. Most lethaeines have claspers that are stout and broadly triangular, with inner and outer projections about equally produced. This is likely to be the plesiomorphic condition, since it is present not only in the Lethaeini, but in the out-groups as well. Several departures from this basic shape represent apomorphic states.

The first of these is the "reversed" clasper shape found in species of *Esuris* (Fig. 6), *Hexatrichocoris* (Fig. 16), *Exomyocara* (Fig. 4), *Myocara* (Fig. 5), and *Paramyocara* (Figs. 2, 3). All of these claspers share the apomorphy of the blade arising on the inner side of the clasper instead of on the outer side, but differences in the areas of attachment, blade and outer projection, as well as differences in the sperm reservoir, indicate that this condition arose three times independently: once in *Esuris,* once in *Hexatrichocoris,* and once in the lineage comprising *Exomyocara, Myocara,* and *Paramyocara.* This peculiar reversed condition also appears to have evolved independently in *Terenocoris nitidus* Slater, an antillocorine.

The second apomorphic clasper shape characterizes all species of *Lethaeus* examined in this study. These claspers (Figs. 29, 31–33) have a long blade, no flange at the area of attachment, and a prominent finger-like inner projection that is strongly deflected toward the base of the clasper.

The genera *Aristaenetus, Lophoraglius,* and *Neolethaeus* form a distinct group based on claspers with an apomorphic shape. Claspers of species in these genera have relatively slender, sickle-shaped blades that curve apically and end in a point (Figs. 34–41). The area of attachment has a prominent flange that imparts a strong concavity

to the inner face of the clasper. The inner projection takes on various modified shapes also. Yet another clearly distinct group consists of species of *Lamproceps, Lampropunctus* and *Valtissius.* These claspers (Figs. 13–15) have apically pointed blades and a small pointed inner projection.

The sperm reservoir is a more complex structure than the clasper. As such, similarity of sperm reservoir morphology is more likely to be synapomorphous and less likely to be homoplasious than is similarity of clasper shape, assuming that at least some of the complex features are apomorphic. Deciding on the plesiomorphic condition, however, is difficult because homologies are uncertain. Based on out-group comparison, my working hypotheses is that a sperm reservoir with most or all of the parts shown in Figures 143 and 144 is closest to the ancestral condition, and that modification of the sperm reservoir has proceeded largely through fusion, reduction or loss of various components.

Like the clasper, the sperm reservoir offers useful characters for recognizing and distinguishing among species. More importantly, many genera have a characteristic sperm reservoir shape, and are thus probably monophyletic. For example, all four species of *Lethaeus* (Figs. 120, 121, 124–129) examined have very similar sperm reservoirs that are unlike other Lethaeini. The complete lack of holding sclerites and the characteristic shape are strong apomorphic characters uniting these species. The type species, *L. africanus,* differs only slightly from the rest of the genus in that the "spur" near the insertion of the conjunctival seminal duct has enlarged to form a pair of flat plates, one on each side of the vesical seminal duct. Presumably the *Lethaeus* type of sperm reservoir has resulted from an extreme reduction of the sleeve, perhaps through an intermediate condition similar to that found in the sperm reservoir of *Noteolethaeus,* which also has a basal "spur" that is perhaps homologous to the one found in *Lethaeus.* This spur may also be homologous with one found in *Xestocoris,* although I have tentatively placed *Xestocoris* with other genera (Group IV below) based on the shape of the wings.

Another example of a genus with a distinct sperm reservoir is *Diniella,* with species united by possessing a fused sleeve and vesical seminal duct. In the sperm reservoir of *D. laeviuscula* (Figs. 106, 107), and *D.* sp. (Fig. 104), this fusion is incomplete. Only about one-fourth of the total number of species in the genus were studied, however.

Several genera, on the other hand, appear composite based on morphology of the sperm reservoir. One such genus is *Neolethaeus.* The three types of sperm reservoirs found in *Neolethaeus* are as different from each other as are the sperm reservoirs of most lethaeine genera. *Neolethaeus aethiopicus* (Figs. 130, 132) and *N. giganteus* (Figs. 131, 133), two African species, have a distinctive synapomorphy in a wide thickened ring or bulge just distal to the opening of the vesical seminal duct (Figs. 132, 133). Undoubtedly these two species are closely related. *Neolethaeus dallasi* (Figs. 140, 141) from Japan, and *N. australiensis* (Figs. 134, 135) lack this thickened ring, and may be more closely related to species in other genera. *Neolethaeus tenebrosus* (Figs. 138, 139) is distinct from the other two types mentioned above, but does not share its distinct morphology with any other species examined thus far.

The two species of *Paragonatas, P. divergens,* the type species (Figs. 48, 57), and *P. costaricensis* (Figs. 53, 54), also have very dissimilar sperm reservoirs. Likewise, the genus *Cryphula* (Figs. 68–72, 75–77) also seems to be composed of two distinct

sperm reservoir types. *Cryphula nitens* (Figs. 68, 69) represents one type, where the sleeve is widely separated from the vesical seminal duct. Another type of sperm reservoir, characterized by prominent corrugations and a sleeve more closely associated with the vesical seminal duct, occurs in the other *Cryphula* species examined (Figs. 70, 71, 75–77). Each of these types also occurs in other Group I genera (see below).

Genera can nevertheless be united into four monophyletic groups based on apomorphic sperm reservoir morphology. The first of these groups, Group I, consists of the following genera: *Cistalia* (Figs. 58, 59), *Coleocoris* (Figs. 49, 50), *Cryphula* (Figs. 68–72, 75–77), *Esuris* (Figs. 51, 52), *Gonatoides* (Figs. 55, 56), *Paragonatas* (Figs. 48, 53, 54, 57), *Petissius* (Figs. 60, 61), and *Rhaptus* (Figs. 73, 74). This group contains species with sperm reservoirs that retain most of the parts shown in Figures 143 and 144. However, if my above hypothesis of character transformation through consolidation and reduction is correct, this group may simply be a phenetic one, based on symplesiomorphy.

Group II genera are characterized by apomorphic, long, v-shaped holding sclerites, and include *Adauctus* (Figs. 116, 117), *Afromydrus* (Figs. 136, 137), *Aristaenetus* (Figs. 93, 94, 114, 118), *Atkinsonianus* (Figs. 110, 111), *Lophoraglius* (Figs. 122, 123), *Neolethaeus* (Figs. 130–135, 138–141), and *Sweetolethaeus* (Figs. 115, 119). Within this sperm reservoir group, *Aristaenetus, Lophoraglius,* and *Neolethaeus* possess claspers of highly modified shapes. It is likely that these three genera shared a common ancestor.

Sperm reservoir Group III comprises the three endemic Australian genera *Exomyocara* (Figs. 64, 67), *Myocara* (Figs. 62, 63), and *Paramyocara* (Figs. 65, 66), and the Neotropical genus *Bubaces* (Figs. 97, 98). The feature that unites these geographically distant genera is the presence of an unusual curled "lip" at the base of the sleeve near the insertion of the conjunctival seminal duct. This lip is greatly expanded in the three Australian genera, giving them their characteristic appearance. The wings may have fused or been otherwise incorporated with the large, heavily sclerotized dorsal structure adjacent to the sleeve that is prominent in all species of this group except *P. punctatum.* Generic limits of the Australian taxa merit review, however, based on examination of the male genitalia. The species of these 3 genera differ from each other as little as do many congeneric species in the Lethaeini, but, more importantly, the sperm reservoir of *Paramyocara iridescens,* the type species, shares the presumed apomorphy of the heavy triangular patch of corrugations with a species of *Exomyocara* (Fig. 67).

The wide, plate-like wings, reduced nature of the sleeve, lack of holding sclerites and overall similarity of shape all seem to indicate a common derivation for Group IV, containing the following genera: *Lamproceps* (Figs. 83, 84), *Lampropunctus* (Figs. 85, 86), *Ptilocamptocera* (Figs. 88, 89), *Valtissius* (Figs. 81, 82) and *Xestocoris* (Figs. 87, 92). *Xestocoris* is enigmatic in that a spur, similar to that found in *Lethaeus* (Figs. 120, 121, 124–129) and *Noteolethaeus* (Figs. 112, 113), is present near the insertion of the conjunctival seminal duct. If this spur proves to be homologous across these taxa, *Lethaeus* and *Noteolethaeus* will be included in Group IV.

Several genera could not be placed in one of the above groups. They are *Austroxestus* (Figs. 108, 109), *Camptocera* (Figs. 90, 91), *Diniella* (Figs. 99–107), *Hexatrichocoris* (Figs. 95, 96), and *Stictolethaeus* (see O'Donnell, 1991).

The clasper and sperm reservoir provide valuable taxonomic characters to distinguish between species, to define monophyletic genera, and to establish sister-group relationships among genera. Difficulties in interpretation of homology and in polarization of character states may be overcome eventually by examining more taxa. It is clear that male genitalia have much to contribute to refining the classification of the Lethaeini.

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A NEW GENUS AND NEW SPECIES OF RHYPAROCHROMINAE (HEMIPTERA: LYGAEIDAE) FROM WESTERN NORTH AMERICA

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Abstract.—A new genus, *Orphnotrechus,* and new species, *O. slateri,* are described. *Orphnotrechus* is placed in the tribe Rhyparochromini and is most closely related to *Peritrechus.* A key to the genera of North American Rhyparochromini is provided.

On the occasion of this Festschrift in his honor, I take pleasure in dedicating a new genus and species to Dr. James A. Slater, my good mentor and friend, in recognition for his contributions to Hemipterology.

Orphnotrechus, new genus
Figs. 1–9

Diagnosis. Thorax and hemelytra dull pruinose, head and abdomen shiny; entire body and appendages dark brown-black with few obscure yellow-brown maculations; pronotal margins carinate, nearly straight; profemora incrassate, armed beneath with two rows of denticles, inner row of two major and eleven minor denticles (Fig.3); claspers with flattened hook (Fig. 6); spermatheca with small bulb, annulate midduct short (Fig. 9).

Description. Smaller in size and narrower in shape than *Peritrechus* (Fig. 1); body sparsely covered with short adpressed sericeous hairs, denser on head and abdomen; thorax and hemelytra dull pruinose, head and abdomen shiny; coarser punctures on posterior lobe of pronotum, corium and clavus, body otherwise finely punctate; coloration of body and appendages dark brown-black with few obscure brown maculations. Head short, almost porrect (Fig. 2), inserted into prothorax nearly to eyes; vertex slightly convex, nearly flat; eyes prominent, antenniferous tubercles very short, not visible from above, lora flat, bucculae low, meeting caudad in blunt V at level of eye. Pronotum laterally carinate, wider than long, length subequal to head, shorter than scutellum, slightly convex above, not constricted laterally or dorsally; lateral margins nearly straight, converging cephalad; anterior angles of pronotum about as wide as width of head across eyes; anterior margin straight, no collar or impression present; posterior margin concave. Scutellum longer than wide, nearly flat, slightly elevated above hemelytra, twice as long as commissure. Hemelytra (Fig. 1) laterally gently convex; three distinct and one irregular row of large punctures on clavus; two rows of punctures on corium along cubital vein, other punctures on corium scattered; membrane slightly shorter than length of corium with four longitudinal veins; median fracture long, exceeding apex of scutellum. Scent gland evapatorium rugulose, covering two-thirds of metapleuron and posterior margin of mesopleuron; peritreme callosity linear, curving caudad; metapleural flange impunctate, set off by row of

punctures. Thoracic sterna moderately convex, without carinae or grooves. Abdominal trichobothrial distribution and sclerite fusion pattern as in other Rhyparochromini. Spiracles three and four dorsal on connexivum. Epipleurites (inner laterotergites) present on segments three to six. Anterior scent gland scar between terga 3 and 4 slightly broader than posterior two scent scars (terga 4–5 and 5–6). Tergum 7 caudally truncate. Sternum 7 with two large anterior apodemes on each side of midline, each apodeme subequal in width to the space between the apodemes. Antennae moderate in length (Fig. 1), first antennal segment just exceeds apex of tylus; segment four a little longer than segment two and equal to length of head; antennae densely clothed with short pale hairs, and sparsely with longer hairs about width of antennae in length; a single short spine on inside of first antennal segment. Legs moderate in length (Fig. 1); profemur (Fig. 3) incrassate, half as wide as long, length equal to width of head and length of scutellum, armed beneath with two rows of small denticles, inner row with two large denticles; other femora moderately incrassate; protibia slightly bowed, with field of small tubercles beneath; coxa without spines; metatibia about as long as width of pronotum, first metatarsomere longer than second and third together; meso- and metatibia with distal row of four short spines. Parandria (p) of male genital capsule (Fig. 4) narrow, pointing cephalad. Clasper (Fig. 6) with hook flattened, blade-like. Spermatheca (Fig. 9) with small bulb and short annulated midduct.

Etymology. Orphnotrechus is derived from Greek *orphnos,* dark and *trechon,* to run, hence, a dark runner, in parallel with *Peritrechus.*

Discussion. Although the nymphs have not yet been found, the scent gland scar between terga three and four is wider than the scent gland scars between terga four and five and five and six, which is characteristic of rhyparochromines with a Y-suture. Therefore I provisionally place *Orphnotrechus* in the Rhyparochromini rather than the Megalonotini, which often has other scent gland patterns. Moreover, the overall morphology is similar to *Peritrechus* Fieber, so much so that I originally thought I had a black *Peritrechus.* However, the description of *Cordillonotus* by Scudder (1984) makes it apparent that a new genus is warranted because the species keys out to *Cordillonotus,* although it lacks the long erect bristle on each anterolateral corner of the pronotum, and the anterior lobe of the pronotum is dull pruinose, not shiny. Moreover, *Orphnotrechus* is almost entirely dark brown-black while *Cordillonotus* has the posterior lobe of the pronotum, corium, legs, and antennae pale, in contrast with the dark scutellum and anterior lobe of the pronotum. *Peritrechus,* a relatively large Holarctic genus of about 25 species, similarly differs in having a contrasting thoracic color pattern, as well as a distinctive yellow V-shaped mark on the apex of the scutellum and a conspicuous pale spot on the base of the membrane. In the available keys to genera of North American Lygaeidae, *Orphnotrechus* does not readily key out to any of the genera. For example, in Slater and Baranowski's (1978) key to the lygaeid genera of North America, *Orphnotrechus* keys closest to *Atrazonotus,* a gonionotine. In Kerzhner and Yachevski's (1964) key to the genera of the Lygaeidae of the European USSR, which has a rich fauna of Rhyparochromini and Megalonotini, in contrast with the small Nearctic fauna, *Orphnotrechus* keys out but poorly to the vicinity of *Lamprodema* Fieber, *Pezocoris* Jakovlev, *Lasiocoris* Fieber and *Hadrocnemis* Jakovlev. At least *Lamprodema* and *Lasiocoris* lack the Y-suture and definitely belong to the Megalonotini. From *Lamprodema* and *Hadrocnemis,*

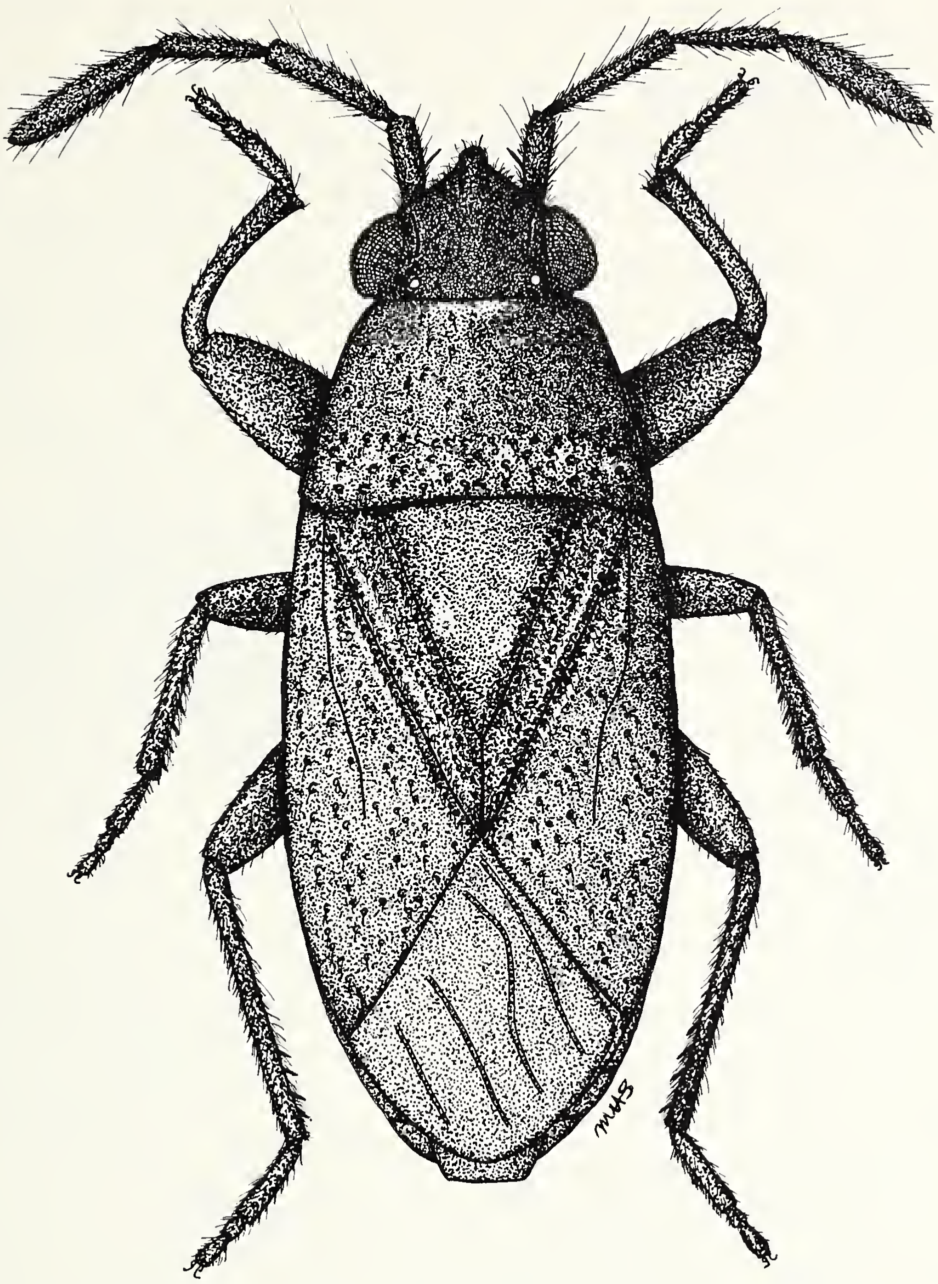
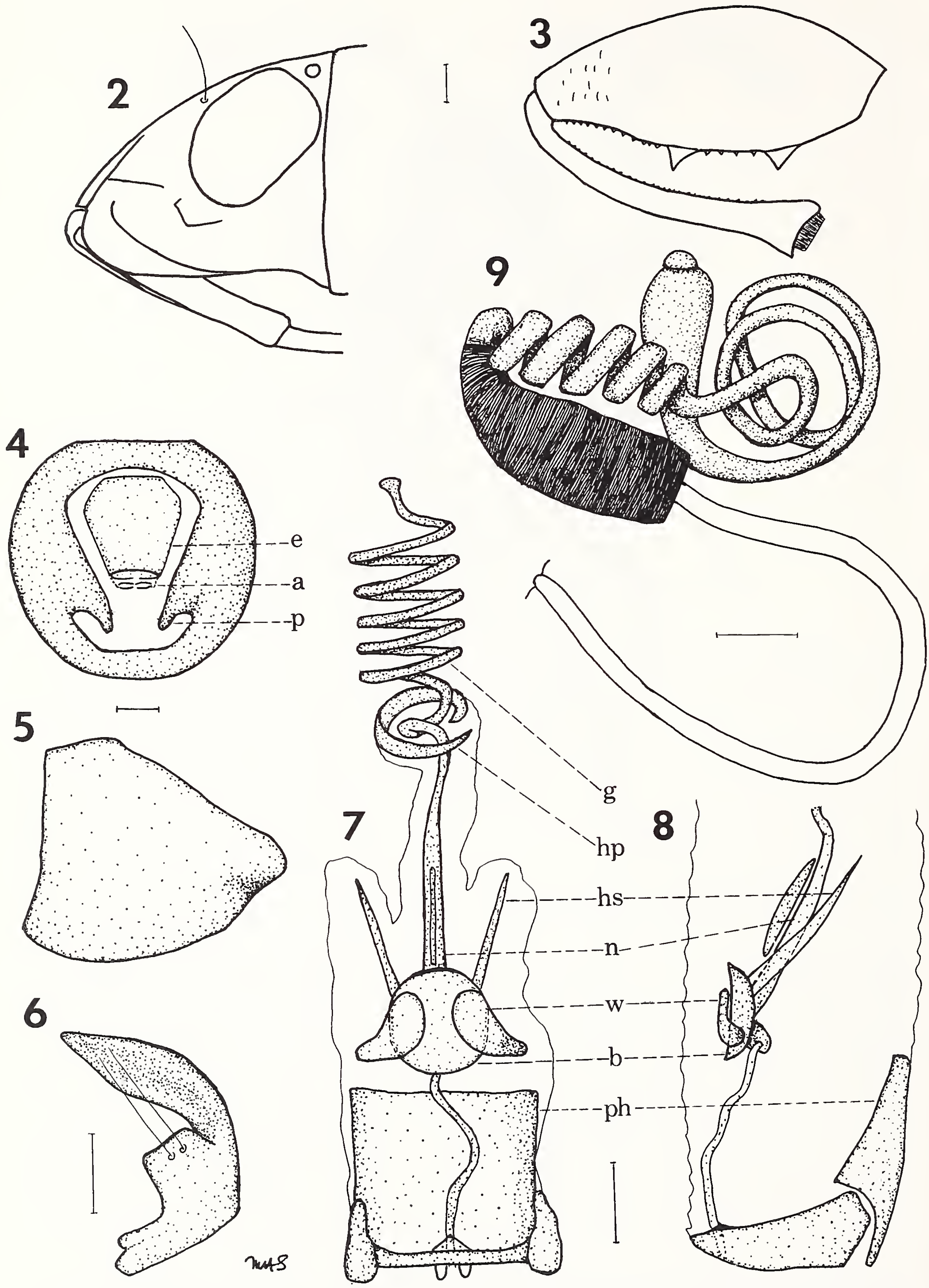


Fig. 1. *Orphnotrechus slateri,* Dorsal view.

Orphnotrechus differs in that the pronotum is dull pruinose above, not shiny, and the posterior lobe of the pronotum is coarsely, not finely punctate. From *Pezocoris, Lasiocoris* and *Hadrocnemis,* which genera Scudder (1962a) called the *Lasiocoris* complex, *Orphnotrechus* differs in that it has no transverse or lateral constriction between anterior and posterior lobe of the pronotum, no long erect dorsal setae on the dorsum, and the hemelytra, scutellum and posterior lobe of the pronotum are dark brown-black, rather than pale in constrast with a dark anterior lobe of the pronotum. *Orphnotrechus* differs from *Orieotrechus* Scudder in not having a V-shape pronotal collar (Scudder 1962b).

The following key will separate the North American genera of Rhyparochromini:

1. Lateral pronotal margins broadly explanate, especially in middle at constriction between anterior and posterior lobes of pronotum .... *Uhleriola* Horvath
– Lateral pronotal margins narrowly carinate, the carina only slightly widened at constriction between anterior and posterior lobes of pronotum 2



Figs. 2–9. *Orphnotrechus slateri.* 2. Head, lateral view. 3. Profemur and protibia, frontal view. 4. Male genital capsule, dorsoposterior view. 5. Genital capsule, lateral view. 6. Left clasper, frontal view. 7. Aedeagus, dorsal view. 8. Ejaculatory reservoir, lateral view. 9. Spermatheca.

2. Anterolateral corner of pronotum with a single long seta; the anterior lobe of pronotum shiny .... *Cordillonotus* Scudder
– Pronotum lacking erect long setae; anterior lobe of pronotum dull pruinose 3
3. Distinct V-shaped pale mark on the apex of the scutellum; carinate lateral margins, posterior lobe of pronotum, and hemelytron pale yellow-brown, in constrast with dark anterior lobe and punctures; mesosternum shiny; lateral margins of pronotum distinctly sinuate .... *Peritrechus* Fieber
– Scutellum, pronotum, and hemelytron dark brown-black with only few obscure maculations; mesosternum pruinose; lateral margins of pronotum nearly straight .... *Orphnotrechus*, n. gen.

Orphnotrechus slateri, new species
Figs. 1–9

Description. Submacropterous male (measurements in millimeters). General coloration of body and appendages dark brown-black; obscure yellow-brown maculations on posterior lobe of pronotum, scutellum, veins of clavus and corium, and trochanters; eyes dark garnet-red. Thorax and hemelytra pruinose, contrasting with shiny head, abdomen and appendages; highly polished iridescent cuticle on inside surface of profemora, posterior surface of antenniferous tubercles, and along lateral carina of pronotum. Coarser punctures on posterior lobe of pronotum, margins of scutellum and corium, punctures (Fig. 1) forming three distinct rows along margins of clavus and anal vein, a weakly defined row in middle of clavus and row on corium along claval suture; fine scattered punctures on anterior lobe of pronotum, middle of scutellum, and thoracic pleura and sterna; dense fine punctures on head and abdominal sterna. Body with fine short adpressed sericeous hairs arising from punctures, hairs more dense and decumbent on head and abdominal sterna; head trichobothria close to eye (Figs. 1, 2); pair of setae on tylus; antennae densely covered with short semi-erect hairs and sparsely with longer hairs, about equal in length to width of antennae; single short spine on inside of first antennal segment; meso- and metatibia and tarsi densely covered with short semi-erect hairs, row of four short spines along distal one-half of mesotibia and one-third of metatibia. Head short, triangular, almost porrect in profile (Fig. 2); width across eyes 0.88, visible length 0.63, preocular length 0.27, interocular distance 0.45; vertex nearly flat, barely higher than eyes. Eyes nude, prominent, almost in contact with pronotal corners, height of eye 0.37. Ocelli moderate in size, dia. 0.06, ocelli and head trichobothria equally close (0.06) to eye. Tylus short, length 0.25, width 0.13, tylar sutures gently converging caudad. Bucculae (Fig. 2) low, widest (0.13) at apex of head, gradually attenuating at level of antenniferous tubercles to become carinae which meet caudad in blunt broad V at level of middle of eye, 0.22 from base of head. Antenniferous tubercles (Fig. 2) very short, hidden from view above (Figs. 1, 2). Pronotum with lateral margins carinate, nearly straight and converging cephalad; anterior margin straight, no collar differentiated, posterior margin gently concave; dorsum slightly convex; anterior lobe set off from posterior

←

Symbols: a, anal sclerites; b, reservoir body; e, epiproct; g, gonoporal process; hp, helicoid process; hs, holding sclerite; n, neck; ph, phallotheca; p, parandria; w, reservoir wing. Scale bars = 0.1 mm.

lobe by coarser punctures; pronotal width at humeral angles 1.29, across anterior angles 0.88; length 0.68, length of anterior lobe 0.49. Scutellum slightly elevated in middle, width 0.77, length 0.88. Hemelytra submacropterous (Fig. 1) not reaching apex of abdomen (in macropter, membrane slightly exceeds apex of abdomen); lateral margins of corium gently convex, covering lateral side of abdomen to tergum 5; length of commissure 0.38; longitudinal distance from apex of clavus to apex of corium 0.75; length of median fracture 1.12; length of membrane 1.32; four veins in membrane. Thoracic sterna and pleura moderately convex; propleural pore present; posterior lobe of propleuron set off by vertical impression; scent gland evapatorium rugulose, covering ⅔ of metapleuron and posterior margin of mesopleuron; callosity of scent gland peritreme linear, curving caudad. Trichobothria in normal pattern for tribe, posterior pair on segment five oblique, on same granulose spot, closer to spiracle (0.06) than to posterior margin of segment (0.10); posterior trichobothria of sternum 6 on separate granulose spots. Width of scent gland scar between terga 3 and 4 0.31, terga 4 and 5 0.27, terga 5 and 6 0.27. Antennal segment 1 exceeds apex of head (Fig. 1), segment 1 subcylindrical, 2 and 3 slightly terete, 4 fusiform; antennal segment lengths: I 0.31, II 0.62, III 0.48 IV 0.67. Labium extends to mesocoxae, first segment does not attain base of head, second attains procoxae; labial segment lengths I 0.51, II 1.08, III 0.34, IV 0.36. Profemur (Fig. 3) incrassate, length 0.90, width 0.38, armed beneath with two rows of denticles, inner row of two major and eleven to twelve minor denticles, outer row of ten small denticles; other femora moderately incrassate. Protibia (Fig. 3) bowed, armed beneath with field of small tubercles. Meso- and metatibia each with one distal row of four spines; length of metatibia 1.13, lengths of metatarsomeres, I 0.37, II 0.07, III 0.14. Genital capsule (Figs. 4, 5) subglobose in dorsoposterior view, posterior of capsule with transverse impression; opening oblique; parandria (p) elongated, pointed caudad; epiproct (e) broad, fused with paraproct to form a flattened operculum-like structure, anal sclerites (a) of segment 11 very slender. Paramere (Fig. 6) with flattened, blade-like hook; shank transversely carinate with two long setae on carina. Aedeagus (Figs. 7, 8) with gonoporal process (g) of four turns, secondary gonopore slightly funnel-shaped; helicoid process (hp) narrow, of one turn; holding sclerites (hs), narrow, attached to reservoir; ejaculatory reservoir with body (b) relatively flat, neck (n) long, wings (w) subtriangular, apices bent down over body; phallotheca (ph) with dorsum and sides desclerotized. (Spermatheca [Fig. 9] with bulb small, relatively small apical cap present; distal duct with three distal coils, 5 helical turns, before widening into a short thick annulated mid-duct; basal duct similar in width and shorter than distal duct.) *Total body length:* 3.85 mm.

Holotype: Submacropterous male. NEW MEXICO: Lincoln Co. Cedar Creek, Ruidoso. Elevation 6,900 ft, August 16, 1970. J. R. and M. H. Sweet. Deposited in American Museum of Natural History.

Paratypes: Same data as holotype. 11 submacropterous males, 4 macropterous males, 10 submacropterous females, 2 macropterous females. Specimens deposited in National Museum of Natural History, British Museum (Natural History), Texas A&M Insect Collection College and J. A. Slater and M. H. Sweet personal collections.

Ecology. The specimens were collected in the ponderosa-pinyon pine altitudinal level at 6,900 feet (2,100 m) at the base of Sierra Blanca Mountain, in the Sacramento Mountains, an isolated range in southwestern New Mexico. The collecting site was

an open flat grassy glade in the forest away from roadsides. The insects were running on the ground in the litter between clumps of grasses. The lygaeids *Ligyrocoris* nr. *diffusus* (Uhler), *Geocoris* sp. and *Uhleriola floralis* (Uhler) were collected with *Orphnotrechus.* The lygaeid populations were low, and *Orphnotrechus* was the most abundant, with approximately four specimens per m^2. In the laboratory, over a period of six months, despite feeding on sunflower seeds, *Orphnotrechus* did not mate or lay eggs which indicates a probable strong reproductive diapause (Sweet, 1964). The ovaries contained no eggs in two females dissected. A subsequent return in 1979 found that the entire area had been recently burned and no additional specimens could be found despite protracted search. Because of its similarity to *Peritrechus,* it is interesting to note that several roadside habitats near the collecting site of *Orphnotrechus* had *Peritrechus* nr. *saskatchewanensis* Barber populations present instead. The *Peritrechus* populations were entirely macropterous which corresponded with the temporary disturbed roadside habitats. This contrasts with the largely submacropterous, very likely largely flightless population of *Orphnotrechus* which was in a more permanent, less disturbed natural habitat, a pattern common in rhyparochromine ground bugs (Sweet, 1964). The populations of *Geocoris, Uhleriola* and *Ligyrocoris* found with *Orphnotrechus* were similarly pterygopolymorphic, and the lygaeid species with *Peritrechus* were all macropterous.

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LIGYROCORIS (HETEROPTERA: LYGAEIDAE: RHYPAROCHROMINAE) MALE-PRODUCED SCENTS SUGGEST A BIOCHEMICAL CHARACTER SYSTEM FOR SYSTEMATIC ANALYSIS

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Abstract.—Gas chromatographic-mass spectral analyses were performed on Tenax®-trapped male specific volatiles (putative pheromones) from sympatrically collected *Ligyrocoris diffusus* (Uhler), *Ligyrocoris sylvestris* (L.) and a group of males intermediate in morphotype, assumed to be hybrids between the two species. Three distinct chemical profiles containing a total of nine insect-derived components were obtained. Two components/peaks were seen in all three chromatograms. Of the remaining seven components, three exhibited by *L. diffusus* were not shown by *L. sylvestris*; similarly four were *L. sylvestris* specific. The volatiles from the presumed hybrid males gave a biochemically hybrid profile, sharing two of the four *L. sylvestris* specific components and all three of the *L. diffusus* specific peaks. Quantitative as well as qualitative differences and commonalities were found among these two *Ligyrocoris* species and the hybrid. These data, in conjunction with preliminary analyses of male volatiles from *Perigenes constrictus* (Say) and *Slaterobius insignis* (Uhler), representatives of two genera both closely related to *Ligyrocoris,* suggest that these male specific scent compounds may be a useful biochemical character system for systematic analysis in the Rhyparochrominae.

Although there are numerous studies of the so-called "defensive secretions" of both nymphal and adult Heteroptera, evidence of pheromone production in the True Bugs is comparatively scant (Aldrich, 1988). Males commonly emit attractants in the Pentatomoidea (Aldrich et. al., 1984; Harris and Todd, 1980; Hibino, 1985; Knight et. al., 1985; Moriya and Masakazu, 1984; Staddon, 1990; Vrkoc et. al., 1977) and also in the Coreidae (Aldrich et. al., 1982). Ondarza et. al. (1986) studying volatiles collected from *Triatoma mazzottii* Usinger (Heteroptera: Reduviidae) implicated a male attractant produced by females and, in the Miridae, females also seem to be the primary attracting or pheromone producing sex (Graham, 1987; King, 1973).

For the family Lygaeidae, work has focused primarily on the large milkweed bug, *Oncopeltus fasciatus* (Dallas) of the subfamily Lygaeinae. Lener (1969) noted a sweet smell from males of *O. fasciatus,* but no such odor from females. Subsequent analysis revealed that this odor is due to a complex of acetates produced in large quantities by the accessory gland of the metathoracic scent gland, which is markedly reduced in females (Games and Staddon, 1973). They suggested that these male-produced acetates are likely to have a role in the sexual activities of the adults. Aller and Caldwell (1979) revealed that extracts from third instar nymphs and young adult females were attractive to both groups. Older females, however, were not only not attracted to these extracts but also yielded an extract that was repellent to the other two groups.

Outside of the Lygaeinae there is little published information on pheromone pro-

duction. Harrington (1972) suggested a pheromonal role for secretions of the metathoracic scent glands of adults and the abdominal scent glands of nymphs for the blissine *Ischnodemus falicus* (Say). In the large subfamily of mostly ground-dwelling Rhyparochrominae, males of *Perigenes constrictus* (Say) produce a peculiar and highly persistent odor associated with the defecations, which characteristically are smeared in long streaks by males (Sweet, 1964). Sweet further suggested that this odor and smearing behavior might play a part in the species' mating behavior.

Within the myodochine genus *Ligyrocoris*, the "songs" produced by stridulating males of two species are distinct (Thorpe, 1979 MS thesis). Yet, surprisingly, *Ligyrocoris diffusus* (Uhler) males silenced by filling the groves of the stridulitrum with nail polish were just as effective as control males in courting and mating with females (Thorpe and Harrington, 1981). Sometime subsequently, I detected a subtle anise-like odor in culture dishes housing isolated male *L. diffusus*. No such odor was apparent in the dishes housing females. Further behavioral observations revealed that this odor was strongest when a male extruded the pygophore in the process of courting a female; males of *Ligyrocoris sylvestris* (L.) also were noted to produce a distinctive odor (Harrington, unpubl.). With pygophore extrusion, the entire abdomen was elongated, exposing the intersegmental membranes and suggesting an odor source such as the sexually dimorphic ventral abdominal gland opening on the VII-VIIIth intersegmental membrane of males of *Pachylis laticornis* (Heteroptera: Coreidae) (Aldrich et. al., 1982) or the male-specific floral and socket type dermal glands found on abdominal sternite IV of *Dysdercus fasciatus* Signoret (Heteroptera: Pyrrhocoridae) (Lawrence and Staddon, 1975).

If these male produced scents are sex pheromones, they are likely to show species-specificity and, thus, provide biochemical characters for systematic analysis. With this reasoning in mind, the study described below was undertaken to investigate the possible utility of these male scent compounds as a character system.

DEDICATION

I am pleased to contribute to this festschrift volume honoring James A. Slater. Beginning when I became his graduate student 25 years ago and continuing in collegial dialogues ever since, Jim has taught me an appreciation for the Lygaeidae, the importance of searching for alternative character systems, and the fundamental value of systematics as the basis for all biological science. Even in retirement, he remains active and productive, teaching, as he does best, by presenting an inspiring example to all of us.

MATERIALS AND METHODS

Insects. L. diffusus is a common lygaeid, often found in numbers along roadsides and in weedy fields throughout much of the United States and Canada from NewFoundland to British Columbia (Slater, 1964). *L. sylvestris* is much less commonly encountered, restricted to more mesic habitats, and typically occurs in sparse populations. It is more northern in distribution; Sweet (1964) regards it as a boreal species. In the central sands portion of Wisconsin these two species occur sympatrically in Juneau and Wood counties.

Collections of *Ligyrocoris* made near Babcock, Wood Co., WI and Necedah, Juneau

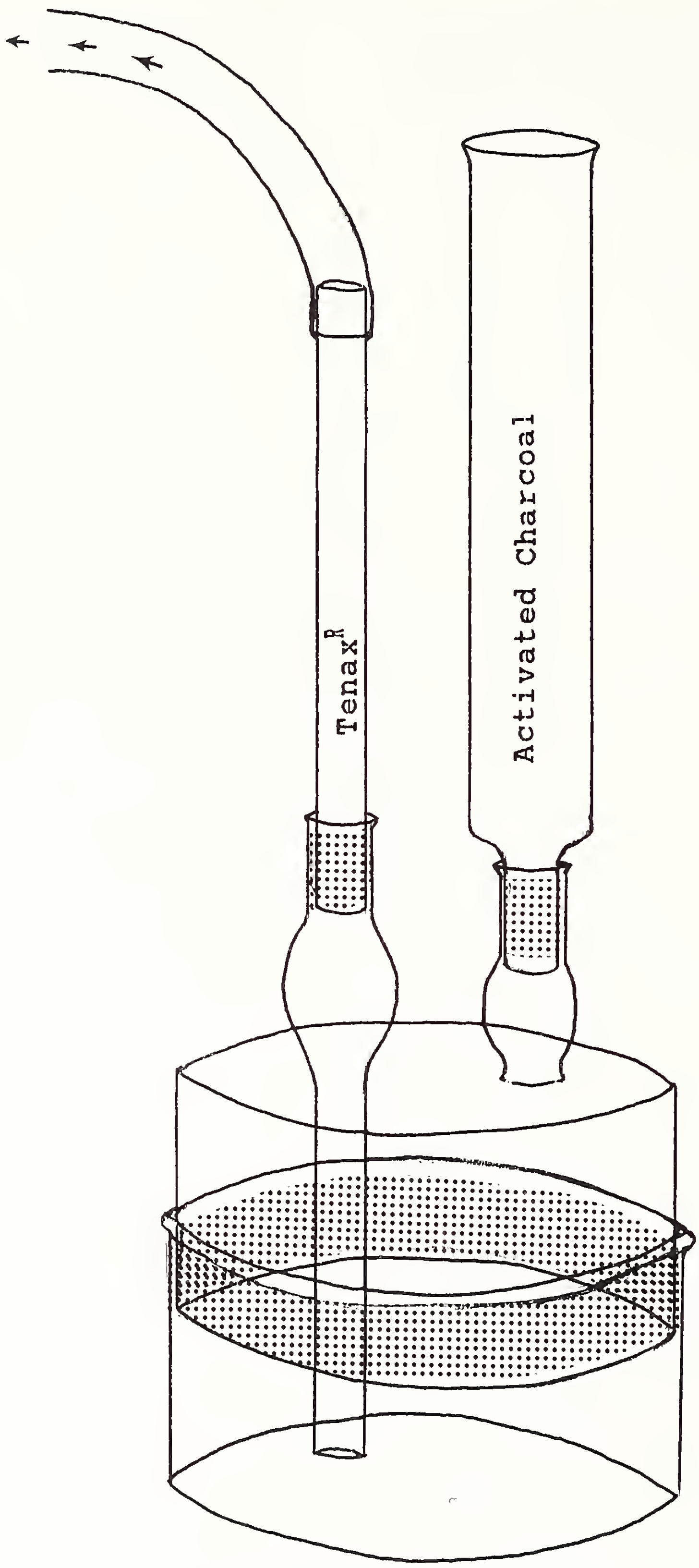

Fig. 1. Modified weighing bottle apparatus for containing insects and collecting volatiles.

Co., WI, in June and July of 1990, included some nymphs which were confusingly intermediate in appearance between the two species. While their coloration, including a distinctive white transverse abdominal band, was more typical of *L. sylvestris,* they had an erect vestiture similar to that of *L. diffusus* but less dense (*L. sylvestris* is virtually devoid of such long upright hairs). When reared to adulthood, these individuals still were not identifiable as either species and represented an intermediate

morphotype; they were tentatively assumed to be hybrids. These presumed hybrids and both *Ligyrocoris* species for this study were provided with water and sunflower seeds, and allowed to mature in the laboratory at 30°C under a 16L:8D photoperiod.

Chemical analyses. Males 1–3 weeks old were contained for scent collection in modified 70 × 33 mm weighing bottles fitted with two chimneys ending in ground glass fittings, one for a filter of activated charcoal and the other for a packed absorbent column containing Tenax® (Fig. 1). Insects were confined with sunflower seeds and water, the latter in a 1 dram vial with dental wicking inserted through a hole in the cap and anchored on the floor of the dish with a small piece of PermaPlast® modeling compound. Scent collections were made by pulling a vacuum regulated by a flowmeter at 15 psi through the apparatus described above. Since stored, unused Tenax® readily absorbs contaminants from the air, blank collection dish controls (i.e., with seed and water but without insects) were run for each Tenax® stock used. A similar volatile collection was made from females of *L. diffusus.*

Each collected scent or control sample was eluted by pouring ca. 3–5 ml of 99⁺% capillary GC n-Hexane (Sigma Chemical, St. Louis, MO) through the column and collecting in a 13 × 100 mm culture tube with a Teflon® lined screw cap. Eluted samples were stored in a standard household refrigerator freezer (ca. −15°C) for 1–4 weeks. Prior to analysis, samples were concentrated under nitrogen to ca 30 μl. For gas chromatography-mass spectrometry analysis, a 1 μl portion of each sample was injected into a 10 m × 0.19 mm i.d., DB-5, bonded phase capillary column (J and W Scientific, Folsom, CA) in a Hewlett-Packard 5890A Gas Chromatograph coupled with a Hewlett-Packard 5970 Mass Selective Detector and a Hewlett-Packard 9133 Data System. Analyses were done using temperature programming, with an initial temperature of 70°C, a final temperature of 200°C and a program rate of 10°C/min. Minor variability in injection procedure may produce minute variations in retention times for the same peak in different runs. To compensate for this variation, and for possible different compounds with the same retention times, mass spectrograms were examined to check the identity of peaks with the apparent same retention times among male odor and control samples. Samples analyzed were approximately 4 insect day equivalents (IDE) of scent output each for *L. diffusus* males and females and *L. sylvestris* males and 2 IDE for the presumed hybrid males.

In an effort to localize a possible source of the observed male odors, eight males of *L. diffusus* were killed by freezing and the bodies separated into head, thorax and abdomen portions. Half of the abdomens were further treated by pulling and stretching to expose the pygophores and intersegmental membranes. Four of each type of body part were soaked for 2 min in hexane and the resulting extracts analyzed as described above for the volatile collections.

RESULTS

Total ion chromatograms for the male odors of *L. sylvestris,* the field-collected presumed hybrids, and *L. diffusus,* are shown in Figure 2A, B, and C, respectively. Comparison of these male odor chromatograms with the Tenax®, seed and water controls revealed that the peaks numbered in Figure 2 are all bug produced compounds. The assemblage of peaks for compounds with retention times greater than 15 min (most readily apparent in Fig. 2A) seem to be minor components found in

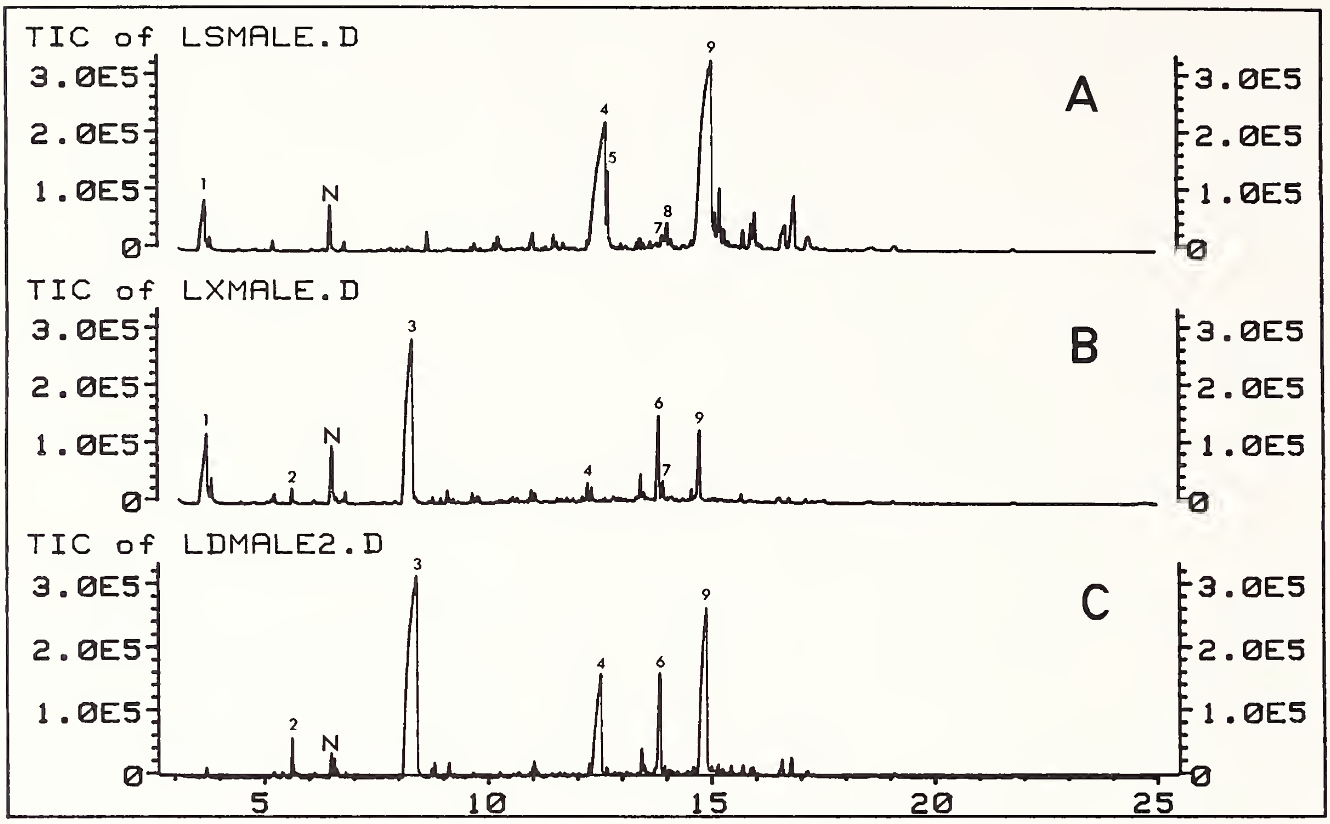

Fig. 2. Total ion chromatograms of male-produced volatiles: A. *Ligyrocoris sylvestris* (L.). B. Presumed hybrids between *L. sylvestris* and *L. diffusus*. C. *Ligyrocoris diffusus*. (Uhler). Numbered peaks represent insect-derived components; N = naphthalene.

all three male group odors; these are not numbered or discussed. The peak labeled "N" (retention time ca. 6.5 min) represents naphthalene, a pervasive and unavoidable contaminant in the atmosphere from the close proximity of the departmental insect collection.

Examination of the profiles in Figure 2 reveals that these male-produced odors involve a complex of compounds. Both species share the compounds represented by peaks 4 and 9, while *L. sylvestris* (Fig. 2A) lacks the compounds represented by peaks 2, 3 and 6 and *L. diffusus* (Fig. 2C) lacks those represented by peaks 1, 5, 7 and 8. Peaks 5 and 8 represent compounds apparently unique to *L. sylvestris,* and not found in the volatiles of either *L. diffusus* or the hybrid males.

Comparison of Figure 2B with the two species' chromatograms reveals that the odors produced by the presumed hybrid males provide a third distinctive chromatogram or profile that is "hybrid" in chemical composition, having some peaks in common with each species but lacking others. The hybrids exhibit peaks 4 and 9 which the two species also have in common. However, it should be noted that the compounds represented by these two peaks are present in much less abundance in the hybrids than in either of the species where they represent major components of the odor complex. In addition, the hybrids share peaks 1 and 7 with *L. sylvestris* and peaks 2, 3 and 6 with *L. diffusus.* The hybrid male profile is closer to that of *L. diffusus* with which it shares peaks 2–4, 6 and 9. Only peaks 1, 4, 7 and 9 are found in common in the complex of compounds exhibited by the hybrids and *L. sylvestris.*

Analysis of the volatiles collected from female *L. diffusus* revealed none of the peaks characterizing the male chromatogram for that species and, in fact, no peaks

occurred in the range of retention times corresponding to the complex of compounds produced by the three male groups studied.

The body part extracts of *L. diffusus* males each showed trace amounts of peaks 3 and 4, with the greatest amount being found, as expected, in the soak of the pulled/stretched abdomens.

DISCUSSION

The strong scent detected olfactorily when a courting male extrudes his pygophore suggested that the odor might be emitted from the pygophore or some other posterior portion of the abdomen. Indeed, among the body part soak extracts, the pulled/stretched abdomens extract gave the largest peaks. However, even these peaks were minor, indicative of very small amounts of the compounds represented by peaks 3 and 4 only and not the other peaks. This negligible yield (which lacks a number of components when compared to the analyzed volatiles of *L. diffusus*) obtained by soaking of body parts suggests that there may not be reservoirs of the compounds making up the male odors but that, instead, these compounds may be stored as precursors and only synthesized upon release. This might also explain why no volatiles were revealed in gas chromatographic analysis of extracts taken from ventral abdominal glands of males of *O. fasciatus* (Aldrich, 1988) and argues for the desirability of a volatile collection method of obtaining suspected pheromones for bioassay. Another reason that volatile collection should be the method of choice is that, where vapor pressures and functionality of pheromone components differ markedly, the liquid phase composition, which is commonly collected directly for a glandular or body part source, may bear little resemblance to the vapor phase or actual pheromone blend (Brand, 1985). Volatile collections are also much cleaner samples, being uncontaminated with other body materials soluble in the same solvent system, and represent the actually emitted compounds in their natural proportions.

Other gas chromatographic analyses of previous volatile collections from male *L. diffusus,* including adults freshly collected from the field and individuals reared in the laboratory for successive generations, indicate the that profile seen in Figure 2C does not vary intraspecifically (Harrington, unpubl.) and suggest that all compounds represented are synthesized by the insects independent of diet (i.e., wild seed choice in the field did not produce a profile different from the restricted laboratory diet of sunflower seeds).

The male odors of both *Ligyrocoris* species studied are sweet and pleasant, not at all like the distinctive buggy odor often produced when Heteroptera are disturbed, which is typically referred to as a "defensive secretion." Aldrich (1988) cautioned that the herding and containment of Heteroptera can cause release of defensive secretions which confound efforts to analyze other volatiles such as possible pheromones. In my experience this is certainly true of some easily agitated species, including a number of Lygaeidae. *Ligyrocoris* species, however, by comparison are very docile, only releasing the characteristic odor of defensive secretion in extreme circumstances such as restraint and gentle squeezing. Thus, I am relatively confident that the volatiles collected for analysis did not include appreciable alarm or defensive secretions.

Preliminary behavioral studies indicate that *L. sylvestris* females are attracted to conspecific male odor extracts applied to absorbent discs, but, surprisingly, *L.*

diffusus females in the same test context are not attracted to male *L. diffusus* odors (J. Fetter, pers. comm.). It is likely that the *L. diffusus* females tested simply were not responsive at the time of assay. However, it is possible that the male scent promotes aggregation in *L. sylvestris,* while some other role(s), such as an aphrodisiac or mate acceptance effect could be envisioned for *L. diffusus.* Further studies are in progress to investigate the influences or roles of male scents, both intra- and intersexually and specifically, in the reproductive behavior of these two species of *Ligyrocoris.* The fact that these scents are produced by the male only suggests a sex pheromone or courtship role, possibly acting as species recognition cues or premating reproductive isolating mechanisms. This supposition is substantiated partially by the species-specificity demonstrated in the current study, although the identification of naturally occurring hybrids raises some question about the efficacy of this chemical communication.

Insect pheromone research naturally has focused on identification, synthesis and deployment of pheromones for control of pest species. Yet, relatively early, it was recognized that, since these compounds or compound blends usually exhibited species specificity, they could be utilized taxonomically for species identification or recognition of cryptic/sibling species (Roelofs and Comeau, 1969). The relative inaccessibility of pheromones, compared to morphological characters, have largely kept these biochemical characters from being used systematically for much other than species identification. The potential for their use in phylogenetic analysis and classification has been underutilized but increasingly sensitive equipment which allows analysis of minute amounts of secretions or volatiles may change this. Also, as isolated studies of the pheromones of a few species continue to accumulate in the literature, these chemical characters will become more available for systematic analyses (Renou et. al., 1988).

In the current study, gas chromatographic-mass spectral analyses of male odors or collected volatiles from two species of *Ligyrocoris* have revealed species specificity in the patterns or profiles presented by the total ion chromatograms and the presumed hybrids gave yet a third distinctive chromatogram. The chromatograms, with verification by mass spectra, clearly show both quantitative/relative abundance and qualitative differences with unique peaks and peaks in common between the species. If those peaks in common are found in other species of *Ligyrocoris* and related genera, as might be anticipated with the heritable biosynthetic pathways suggested by the hybrid data, then the complex of compounds making up these male-produced scents should provide a very good biochemical character system to corroborate or refute systematic analyses based on morphological character systems. Preliminary analyses of male volatiles from *Perigenes constrictus* (Say) and *Slaterobius insignis* (Uhler), two other genera belonging to the same monophyletic lineage as *Ligyrocoris* (Harrington, 1980), show distinct profiles including some peaks in common (possible synapomorphies) suggesting that the male specific volatiles of these bugs have utility for systematics. Further work in pursuing this potential and behavioral studies of the biological role(s) of these male specific scents are in progress.

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HEMIPTERA-HETEROPTERA FROM MEXICO XLIII. A NEW GENUS AND THREE NEW SPECIES OF NEOTROPICAL MICRELYTRINAE (ALYDIDAE) COLLECTED ON BAMBOOS

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Abstract.—A new genus of Micrelytrinae (Alydidae) is erected and three new species collected in Mexico are described. Its resemblance with *Bactrophya* Breddin, *Bactrocoris* Kormilev, and *Slateria* Ahmad, as well as its relationship within the Micrelytrinae, are discussed. The host plant of each species is a *Guadua* spp. (Bambuseae). A key is given to distinguish the known species. Illustrations include a dorsal and lateral view of the head, the antennal segments, and details of the pygophore and the genital plate of the female.

During a revision of the Mexican Micrelytrinae (Alydidae) (Brailovsky and Zurbia, 1979), I had the opportunity of examining several unusually slender specimens. They obviously belonged to the Micrelytrinae, because of the medioposterior spine on the pygophore, the small bucculae, a nonsulcate hind tibia, and labial segment II conspicuously longer than labial segments III and IV together.

Each of the species described in the present paper was collected on bamboos, belonging to the genus *Guadua* (Bambuseae), confirming the grass feeding preferences of the subfamily.

The following abbreviations are used in the text: American Museum of Natural History, New York (AMNH); British Museum of Natural History (BMNH); Instituto de Biologia de la Universidad Nacional Autonoma de Mexico (IBUNAM); Texas A&M University (TAMU); University of Karachi (UK).

All measurements are in millimeters.

Bactrophyamixia, new genus

Description. Body slender, elongate and linear. **Head.** Remarkably elongate, longer than pronotum and parallel sided; juga strongly developed, exceeding the tylus for more than 80% of their total length and confluent over most of that length; juga wider and stouter on proximal three fourths, narrowing distally, apically acute and in lateral view decurved or nearly straight (1, 2, 5, 6, 10, 11, 14, 15, 19, 20); ocelli small, interocellar space less than the distance from eye to ocellus; pit anterior to ocellus conspicuous; frons with the median longitudinal sulcus distinctly longer than distance between ocelli; eyes relatively small, hemispherical, in lateral view located below the frontal surface; antenniferous tubercles unarmed; antennal segment I weakly swollen or dorsoventrally depressed and sulcate (Figs. 23–25); antennal segment II and III long, slender; segment IV slender, slightly curved, and fusiform; antennal segments I–III with long, erect slender setae, segment IV with shorter semierect setae; antennal segment I subequal in length to IV or conspicuously shorter; bucculae small,

confined to the apical third of the head; labium reaching from posterior border of metasternum to anterior margin of abdominal sternum III; labial segment I reaching prosternum; labial segment II longer than segments III and IV together. **Thorax.** *Pronotum.* Subrectangular, parallel, sided, unarmed, not declivent, and longer than wide; densely punctate, the callar region somewhat rugose or nodulose; humeral angles obtuse and rounded; propleuron heavily punctate, mesopleuron and metapleuron with scattered punctures; prosternum concave; mesosternum and metasternum smooth and with a deep median longitudinal sulcus; metathoracic scent glands opening into coxal cavities, with the anterior scent gland lobe elongate and oriented longitudinally, the posterior lobe shorter and oriented transversely. *Legs.* Unarmed; tarsal segment I longer than segments II and III together; femora and tibiae with long, slender, erect setae. *Scutellum.* Longer than wide, unarmed, and irregularly punctate. *Hemelytra.* Clavus and corium with large irregularly placed punctures; costal margin of corium extending more than ⅔ parts of length of membrane; membrane reaching from posterior margin of abdominal tergum VI to posterior margin of the abdominal tergum VII. **Male genitalia.** *Pygophore.* Posteroventral border depressed or not and with a large, acute, medioposterior spine, with the parameres not attaining apex of spine (Figs. 7, 21) or paramere arrow-shaped and exceeded by the spine (Fig. 16); pygophore in lateral view as in Figures 9, 18, and 26, dorsal view as in Figures 8, 17, and 22. **Female genitalia.** Inflated or not; seventh abdominal sternum posteriorly entire; first gonocoxae somewhat squared, with inner margin sinuately emarginate and outer margin sinuate or straight (Figs. 3, 4, 12, 13).

Type species. Bactrophyamixia slateri, new species.

Etymology. Named for the similarity of its appearance to *Bactrophya*; feminine.

Distribution. Mexico.

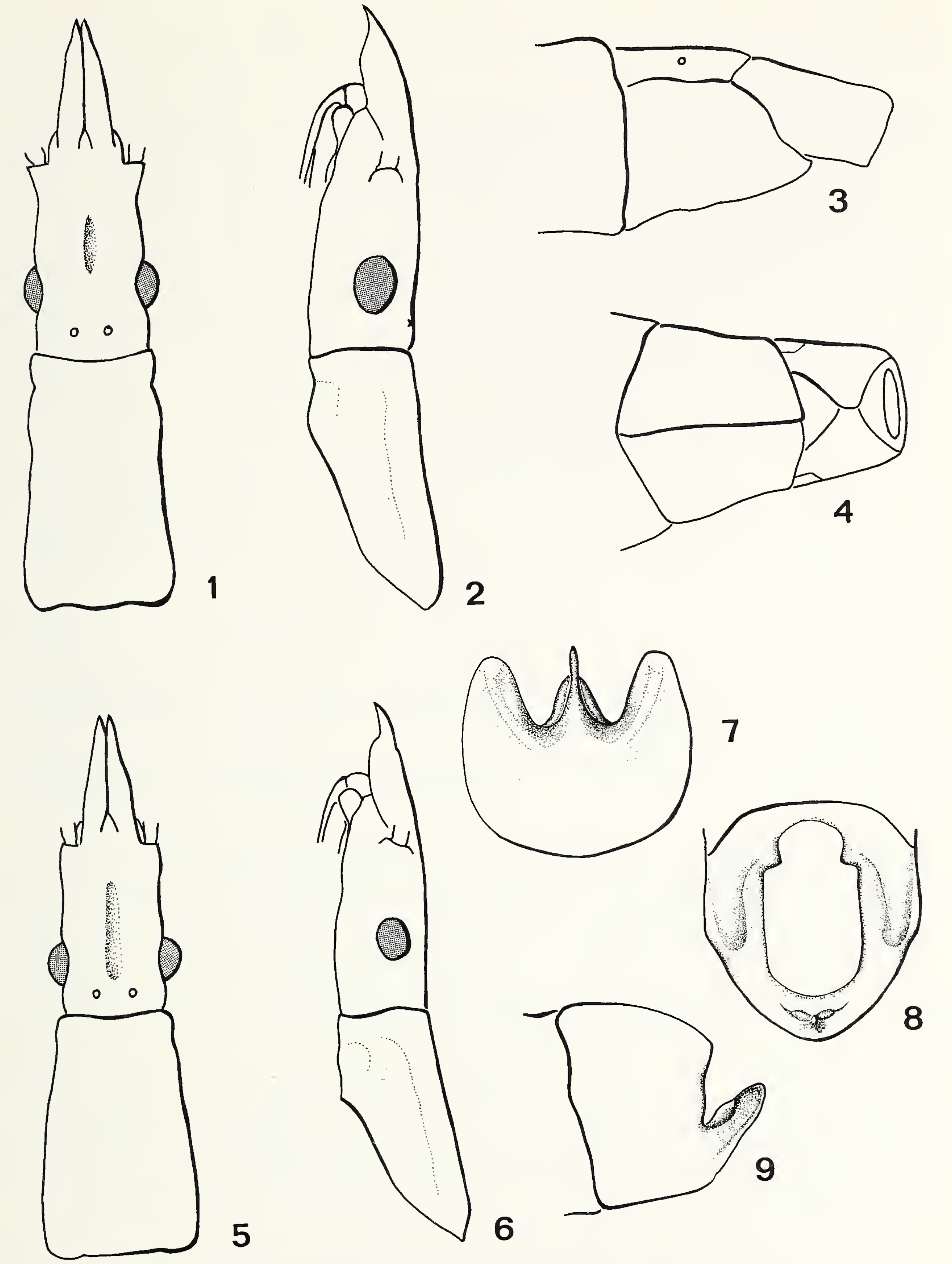
Discussion. Bactrophyamixia is distinctive within the subfamily Micrelytrinae by virtue of the extraordinary development of the juga, which greatly exceed and are confluent in front of the tylus, with the distal third acuminate and forming a straight or decurved projection, together with the pronotum and scutellum totally unarmed.

In *Bactrophya* Breddin and *Bactrocoris* Kormilev, both from South America, the juga are well developed, elongate and hide the tylus and the head is longer that the pronotum, but the distal third of the juga is never acuminate as typical of *Bactrophyamixia.*

The new genus also resembles *Slateria* Ahmad, described from Burma (Ahmad, 1965). In both genera the body is linear, the head elongate and longer than the pronotum, and the juga are strongly developed. Despite these similarities, *Bactrophyamixia* can easily be separated from *Slateria.* In the latter the juga are separated from one another by an enormously developed tylus, which is produced and pointed in front of the juga like a beak, and the first antennal segment has a strong dorsolateral spine distally which is absent in the *Bactrophyamixia.*

Bactrophyamixia slateri, new species
Figs. 1–9, 23

Description. Individuals of relatively large size, slender, elongate, with the antennal segment I swollen throughout and little longer than or subequal to segment IV. **Dorsal**



Figs. 1–9. *Bactrophyamixia slateri,* new species. Figs. 1–4. Female. 1. Head and pronotum in dorsal view. 2. Head and pronotum in lateral view. 3. Genital plates in lateral view. 4. Genital plates in ventral view. 5–9. Male. 5. Head and pronotum in dorsal view. 6. Head and pronotum in lateral view. 7. Pygophore in frontal view. 8. Pygophore in dorsal view. 9. Pygophore in lateral view.

coloration. Head, pronotum, scutellum, entire hemelytra, connexival segments, and antennal segments I to III pale orange yellow; ocelli reddish; dorsum of abdomen pale brownish; punctures of scutellum, clavus, and corium obscurely orange. **Ventral coloration.** Head, mesosternum, metasternum, and abdominal sternum pale yellow cream; prothorax, mesopleuron, metapleuron, and legs pale orange yellow; labium pale orange yellow, with a few scattered red markings and with segment IV mostly black; mid portion of abdominal sterna II to VII black. Antennal segment I terete and swollen throughout and little longer or subequal to segment IV (Fig. 23); labium reaching the posterior margin of metasternum; membrane of hemelytra reaching the anterior margin of the seventh abdominal tergum. **Genitalia.** *Male. Pygophore.* Posteroventral border not depressed, with a large acute, medioposterior spine with the apical third simple and acute, the parameres not attaining the apex of the spine (Fig. 7); pygophore in dorsal view as in Figure 8; pygophore in lateral view as in Figure 9. *Female.* Genital plates not inflated (Figs. 3–4).

Measurements. Male. Length head: 2.92; interocellar space: 0.24; width across eyes: 1.40; interocular space; 0.88; length antennal segments: I, 4.16; II, 3.60; III, 2.60; VI, 4.12; length labial segments: I, 2.40; II, 2.56; III, 0.40; IV, 0.84. Length pronotum: 2.28; width across frontal angles: 1.16; width across humeral angles: 1.52. Length scutellum: 1.20; width: 0.88. Total body length: 17.20.

Female. Length head: 3.22; interocellar space: 0.28; width across eyes: 1.56; interocular space: 1.04; length antennal segments: I, 4.40; II, 3.92; III, 2.64; IV, 3.96; length labial segments: I, 2.72; II, 2.84; III, 0.44; IV, 0.84. Length pronotum: 2.36; width across frontal angles: 1.32; width across humeral angles: 1.60. Length scutellum: 1.16; width: 0.74. Total body length 16.54.

Holotype male. MEXICO: GUERRERO: km. 20 carretera Chilpancingo-Omilteme, 29.I.1982, A. Ibarra. Collected on *Guadua* sp. (Bambuseae). Deposited in IBUNAM.

Paratypes. MEXICO: GUERRERO: km. 5 carratera Chilpancingo-Omilteme, 26.XI.1981. H. Brailovsky y E. Barrera. Collected on *Guadua* sp. (Bambuseae). Two males, one female. Deposited in IBUNAM. MEXICO: GUERRERO: Chapa, 5.III.1987. E. Barrera, H. Brailovsky, y L. Cervantes. Collected on *Guadua* sp. (Bambuseae). Three females, one male. Deposited in AMNH, BMNH, and IBUNAM. MEXICO: GUERRERO: km. 73 carretera Cuernavaca-Iguala, 30.I.1982. E. Barrera. Collected on *Guadua* sp. (Bambuseae). One female. Deposited in IBUNAM. MEXICO: GUERRERO: Teloloapan. 22.X.1983. H. Brailovsky y E. Barrera. Collected in *Guadua spinosae* (Sw.) McClene (Bambuseae). Two females. Deposited in IBUNAM. MEXICO: GUERRERO: km. 11 carretera Chilpancingo-Chichihualco, 29.XI.1981. H. Brailovsky. Collected in *Guadua* sp. (Bambuseae). One female. Deposited in IBUNAM.

Discussion. Distinguished by the dimensions and form of the male genitalia (Figs. 7–9), the genital plates of the female not swollen (Fig. 3), and antennal segment I swollen throughout and little longer or subequal in length to antennal segment IV (Fig. 23).

Etymology. Named for Dr. James A. Slater, in recognition of his distinguished services toward the advancement of knowledge of the family Lygaeidae and for the many years of friendship.

Bactrophyamixia antennata, new species
Figs. 10–18, 24

Description. Individuals of relatively large size, slender, elongate, linear, with antennal segment I dorsoventrally depressed and sulcate and conspicuously shorter than segment IV. **Dorsal coloration.** Head, pronotum, entire hemelytra, connexival segments, abdominal dorsum, and antennal segments I to III pale yellow; antennal segment IV brownish with the basal third and distal third pale yellow; pronotal disc with few pale yellow-cream spots; scutellum pale yellow green; punctures of scutellum, clavus and corium obscurely orange. **Ventral coloration.** Head and abdomen pale yellow; thorax, lobes of the metathoracic scent glands, coxae, trocanters, and femora pale yellow and sprinkled or not with pale green; tibiae and tarsal segments pale orange yellow; labial segments I and II pale yellow, III castaneus and IV mostly black; posterior border of abdominal sterna IV-VI yellow or brownish. Antennal segment I dorsoventrally depressed and sulcate and conspicuously shorter than IV (Fig. 24); labium reaching the anterior margin of abdominal sternum III; membrane of hemelytra reaching the posterior margin of abdominal tergum VI. **Genitalia.** *Male. Pygophore.* Posteroventral border not depressed, with a large, acute medioposterior spine, with the apical third arrow-shaped (Fig. 16); pygophore in lateral view as in Figure 18; pygophore in dorsal view as in Figure 17. *Female.* Genital plates inflated (Fig. 12).

Measurements. Male. Length head: 3.20; interocellar space: 0.20; width across eyes: 1.36; interocular space: 0.88; length antennal segments: I, 4.62; II, 3.28; III, 2.60; IV, 6.10; length labial segments: I, 2.72; II, 2.88; III, 0.36; IV, 0.76. Length pronotum: 2.04; width across frontal angles: 1.12; width across humeral angles: 1.48. Length scutellum: 1.12; width: 0.92. Total body length: 17.56.

Female. Length head: 3.64; interocellar space: 0.20; width across eyes: 1.60; interocular space: 1.04; length antennal segments: I, 4.04; II, 3.28; III, 2.64; IV, 5.16; length labial segments: I, 3.00; II, 3.00; III, 0.44; IV, 0.80. Length pronotum: 2.24; width across frontal angles: 1.72; width across humeral angles: 1.72. Length scutellum: 1.16; width: 0.92. Total body length: 18.10.

Holotype male. MEXICO: CHIAPAS: Boca Lacantum (Rio Usumacinta), 25.V.84. E. Barrera and M. Garcia. Collected in *Guadua* sp. (Bambuseae). Deposited in IBUNAM.

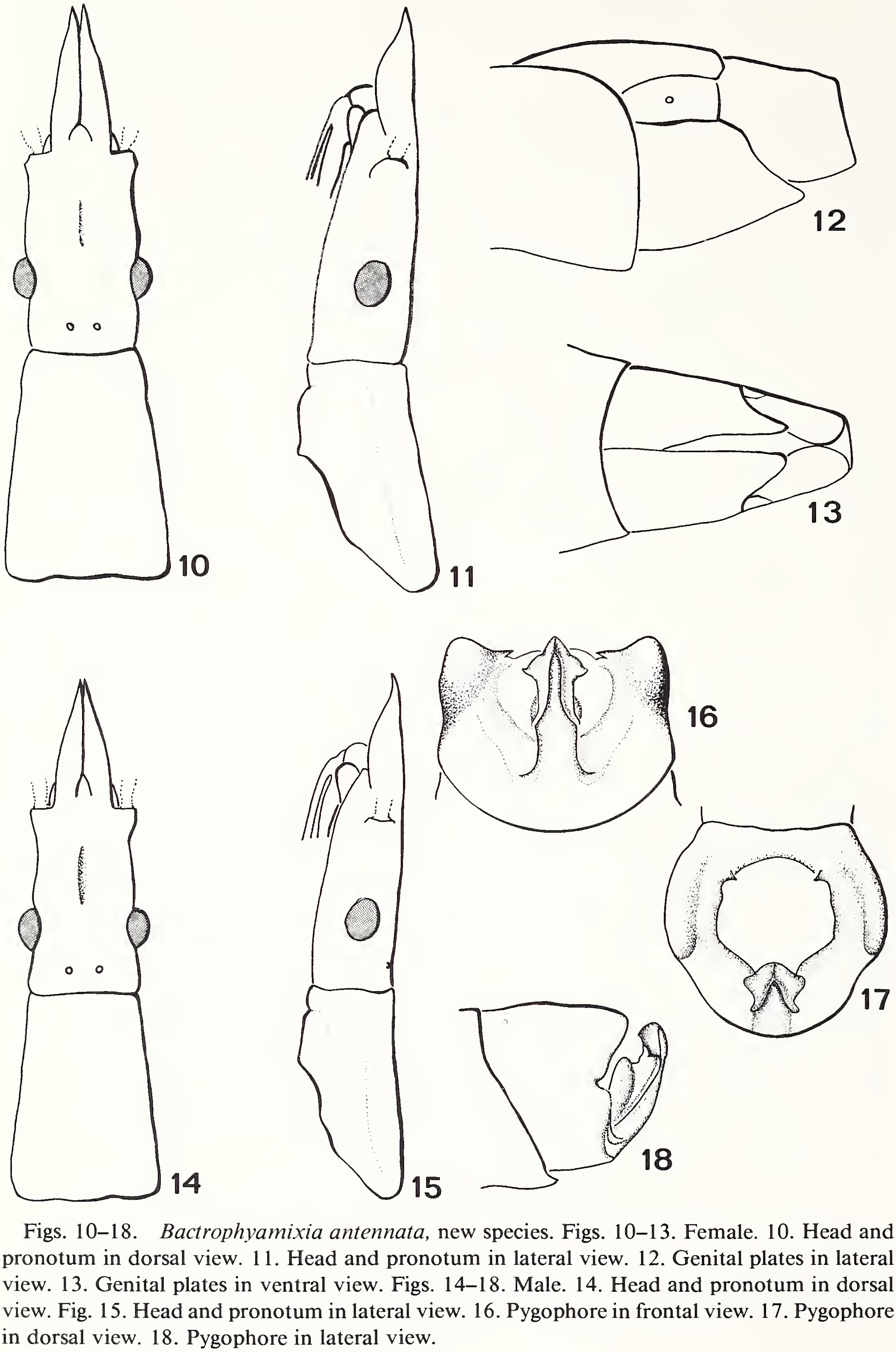
Paratype. Female. Same data as holotype. Deposited in IBUNAM.

Discussion. Recognized by the dimensions and the form of the pygophore (Figs. 16–18), the inflated genital plates of the female (Figs. 12–13), and antennal segment I depressed, sulcate, and conspicuously shorter than segment IV (Figs. 23–25).

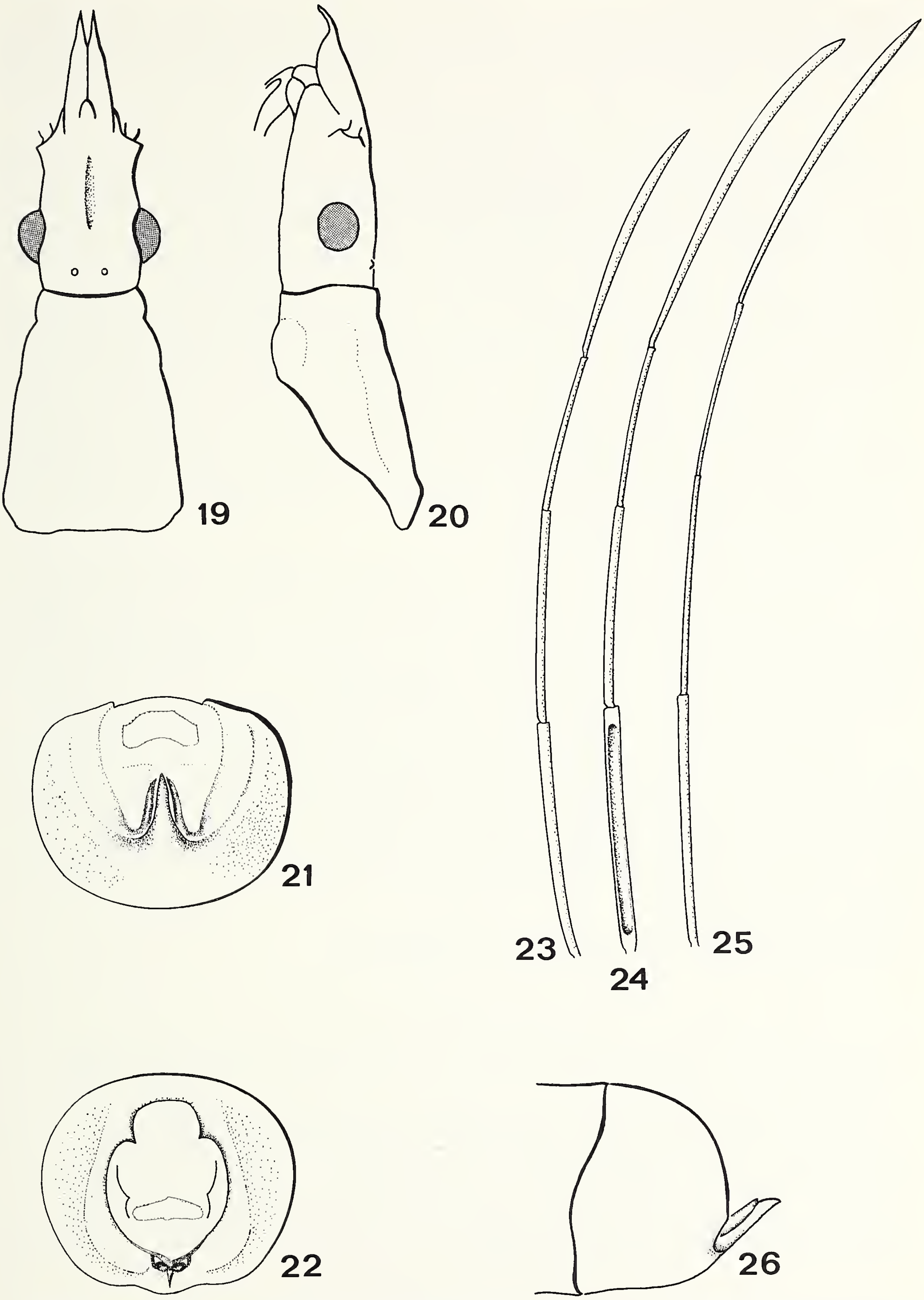
Etymology. Named for the remarkable structure of antennal segment I.

Bactrophyamixia bambusicola, new species
Figs. 19–22, 25–26

Description. Individuals of relative large size, slender, elongate, with antennal segment I swollen throughout and conspicuously shorter than segment IV. **Dorsal**



Figs. 10–18. *Bactrophyamixia antennata,* new species. Figs. 10–13. Female. 10. Head and pronotum in dorsal view. 11. Head and pronotum in lateral view. 12. Genital plates in lateral view. 13. Genital plates in ventral view. Figs. 14–18. Male. 14. Head and pronotum in dorsal view. Fig. 15. Head and pronotum in lateral view. 16. Pygophore in frontal view. 17. Pygophore in dorsal view. 18. Pygophore in lateral view.



Figs. 19–22, 26. *Bactrophyamixia bambusicola,* new species. 19. Head and pronotum in dorsal view. 20. Head and pronotum in lateral view. 21. Pygophore in frontal view. 22. Pygophore in dorsal view. 26. Pygophore in lateral view. Figs. 23–25. Antennal segments. 23. *Bactrophyamixia slateri.* 24. *Bactrophyamixia antennata.* 25. *Bactrophyamixia bambusicola.*

coloration. Head and pronotum pale orange yellow, with longitudinal yellow cream stripe laterally and isolated cream spots on the pronotal disc; antennal segments I to III orange, segment IV pale yellow on basal half and brownish on apical half; scutellum, clavus, and corium pale orange yellow with a brownish stripe on tergum VI. **Ventral coloration.** Head and abdominal sternum III to VI pale orange yellow; abdominal sterna VII and VIII and pygophore mostly brownish black; labial segments I to III pale yellow and IV pale orange with the apical third black; mesosternum, metasternum, lobes of the metathoracic scent glands, and a small spot on the acetabulae of the three pairs of legs pale yellow cream; prothorax, mesopleuron, and metapleuron pale yellow with the punctures obscurely orange; coxae, trochanters, and basal third of femora pale yellow, the rest of the legs orange. Antennal segment I terete and swollen throughout and conspicuously shorter than segment IV (Fig. 25); labium reaching the anterior margin of the abdominal stergum III; membrane of hemelytra reaching the posterior margin of abdominal tergum VII. **Genitalia.** *Male. Pygophore.* Posteroventral border depressed in lateral view, with a large, acute medioposterior spine, the apical third simple and acute, with the paramere reaching to just below the apex of spine (Fig. 21); pygophore in lateral view as in Figure 26; pygophore in dorsal view as in Figure 22.

Measurements. Male. Length head: 2.80; interocellar space: 0.20; width across eyes: 1.56; interocular space: 0.96; length antennal segments: I, 4.84; II, 3.83; III, 3.04; IV, 5.64; length labial segments: I, 2.60; II, 2.68; III, 0.44; IV, 0.88. Length pronotum: 2.32; width across frontal angles: 1.24; width across humeral angles: 1.84. Length scutellum: 1.44; width: 1.00. Total body length: 17.15.

Holotype male. MEXICO: OAXACA: Portillo del Rayo, 31.XI.1987. Ernesto Barrera. Collected on *Guadua* sp. (Bambuseae). Deposited in IBUNAM.

Discussion. Most similar in structure and coloration to *B. slateri.* In *B. bambusicola* antennal segment I is conspicuously shorter than segment IV, the anterolateral margin of the pronotum has a yellow cream stripe that constrasts with the pale orange yellow color of the pronotal disc and the pygophore is distinctive (Figs. 7–9, 21, 22, 26). In *B. slateri* antennal segment I is little longer than or subequal in length to segment IV (Figs. 23 and 25).

Etymology. Named for its occurrence on bamboos.

KEY TO *BACTROPHYAMIXIA* SPECIES

1. Antennal segment I depressed and sulcate (Fig. 24); pygophore with lateral border markedly exposed (Fig. 18) .... *B. antennata,* new species
– Antennal segment I swollen throughout and never depressed and sulcate (Figs. 23 and 25); pygophore with lateral border rounded and not exposed (Figs. 9 and 26) 2
2. Antennal segment I conspicuously shorter than segment IV; pygophore with the posteroventral border depressed (Fig. 26) .... *B. bambusicola,* new species
– Antennal segment I a little longer or subequal to segment IV; pygophore with the posteroventral border not depressed (Fig. 9) .... *B. slateri,* new species

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A REVISION OF THE LEPTOPODOMORPHA (HETEROPTERA) OF MADAGASCAR AND NEARBY INDIAN OCEAN ISLANDS

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Abstract. — Previous works on the Leptopodomorpha of Madagascar and nearby Indian Ocean islands are reviewed, keys to genera and species are provided, and the following new taxa are described: *Leptopoides* n. gen. to hold *Leptopus horvathi* Drake and Hottes (type-species) and *Leptopoides poissoni* n. sp.; *Erianotoides oculatus* n. gen., n. sp. (Leptopodidae); *Mascarenisalda* n. gen. to hold *Saldula mametiana* Drake (type-species); *Capitonisaldoida cryptica* n. gen., n. sp.; *Rupisalda slateri* n. sp., *Rupisalda vincenti* n. sp., and *Rupisalda atra* n. sp. (Saldidae). Additional descriptive notes are given for *Leptopoides horvathi* (Drake and Hottes) and *Saldula madagascariensis* Cobben. Other described taxa occurring in the region are discussed.

Our knowledge of the Leptopodomorpha of Madagascar, the Comores and the Mascarene Islands is poor, as noted by Paulian in his summary of the fauna of Madagascar and nearby islands (1961:223), consisting of isolated descriptions of a few species based on scanty material. Collections made in recent years, however, have revealed that Madagascar and the surrounding Indian Ocean islands have a rich shore bug fauna containing many endemic genera and species. In this revision we review previous works, provide keys to genera and species, and describe two new genera and two new species of Leptopodidae plus two new genera and four new species of Saldidae. Most of the material discussed below was collected jointly during an expedition to Mauritius and Madagascar supported in part by the National Geographic Society, and by the junior author during an expedition to Aldabra and Cosmoledo Atolls, supported by the Smithsonian Insitution's Aldabra Project and the Seychelles Islands Foundation.

All measurements are in millimeters. Institutional abbreviations and information on the deposition of type material is contained in the acknowledgments section.

FAMILY LEPTOPODIDAE

The last revision of the family Leptopodidae was provided by Horvath (1911). Germane to this project, he described the genus *Martiniola* and furnished a key to world genera. His key was flawed (e.g., erroneously states that the fore femur of *Valleriola* has only one row of spines) and did not contain all genus-group names now known so a new key is provided below that includes the new genus-group names described herein and the subgenus *Pseudopatapius* Drake and Hoberlandt 1951. The key is based on material in the Polhemus collection representing all known leptopodid genus-group taxa of the Old World. In Leptopodidae, the first visible rostral segment

is actually segment two, which should be borne in mind when comparing other keys to the one given here. The nomenclature follows the latest tribal level conspectus of Schuh, Galil and Polhemus (1987), wherein the tribe Leptopodini includes all of the taxa treated by Horvath (1911) as belonging to the family Leptopodidae.

All members of the Old World tribe Leptopodini have been shown to possess a stridulatory mechanism involving the first abdominal tergite and the vannus of the posterior wing, an apomorphy separating Leptopodini from Leotichiini (Pericart and Polhemus, 1990). The extensive discussion and figures of these structures, given for all of the Madagascar genera, is not repeated here.

KEY TO THE GENERA OF LEPTOPODINI

1a. First visible (second) segment of the rostrum armed on each side with two long and fine spines, second segment without spines or at most with setiform spines, not dilated 2

1b. First two visible segments of the rostrum armed with stout spines, the second segment dilated on its inner side 5

2a. Third antennal segment very much longer than second; entire length of anterior tibia with numerous very short spines (setiform or stout) in one densely packed regular row; head without dorsal spines, or at most with slender setiform spines 3

2b. Third antennal segment a little longer than second; spines of the anterior tibia less numerous and less densely packed, not more than about 10 in each of one or two rows; head with stout dorsal spines at least on clypeus and frons 4

3a. Third antennal segment more than 3 times as long as second; head across eyes clearly wider than pronotum; pronotal calli set with 4 (2+2) thick conical spines; fore tibia set with yellowish setiform spines .... *Erianotoides* n. gen.

3b. Third antennal segment about 2 to 2.3 times as long as long as second; head across eyes at most approximately equal to width of pronotum (usually); pronotal calli not spinose, or at most set with slender setiform spines; fore tibia set with stout dark spines .... *Valleriola* Distant

4a. Anterior tibia provided with only one row of rather short spines; the spines of the anterior femora directed almost perpendicularly beneath; pronotum and hemelytra set with long soft hairs .... *Erianotus* Fieber

4b. Anterior tibia armed with two rows of long spines, these spines as well as those of the anterior femora are divergent, those of the anterior row being directed forward and those of the posterior row to the rear; pronotum and hemelytra bristling with setiform spines .... *Martiniola* Horvath

5a. Second antennal segment longer and thinner than the first, the third two to three times as long as second; first cell or inside of the membrane subequal to or only a third or a fourth shorter than the second 7

5b. Second antennal segment shorter, almost as thick as the first, the third almost ten times as long as second; first cell of the membrane greatly shortened, three-fourths shorter than the second .... *Patapius* Horvath 6

6a. Eyes subglobose, set with long stout spines .... subgenus *Patapius* Horvath

6b. Eyes larger, globose, set with slender setiform spines .... subgenus *Pseudopatapius* Drake & Hoberlandt

7a. Eyes with at most short insignificant setae; clypeus and vertex of head without spines; fore tibia set with slender dark spines beneath, plus two stout anteriorly directed spines basally; first (inner) cell of membrane extending posteriorly almost as far as second; fourth (outer) cell of membrane slightly shorter than third; venation of fore wing as in Figure 2 .... *Leptopoides* n. gen.

7b. Eyes with short slender spines; clypeus and vertex of head set with spines; fore tibia set with two divergent rows of long stout spines directed anteriorly and posteriorly; first cell of membrane one-third to one-fourth shorter posteriorly than second; fourth cell of membrane about ⅔ as long as third; for venation of fore wing, see figure 21B, J. Polhemus 1985 (p. 41) .... *Leptopus* Latreille

Erianotoides, new genus
Figs. 1, 6–10

Description. Small, elongate, length 3.33–3.53 mm; maximum width (across posterior portion of hemelytra) 0.97–1.00 mm. Ground color leucine to pale whitish tan, sparingly marked with brown; venter leucine. Head, anterior part of pronotum, venter with short to moderate length pale setae. Frons glabrous; pronotum except for callus, hemelytra except for membrane, alveolate. Pronotal calli raised, mammilose, each callus with 2 very stout tapered dorsally directed spines, each sheathed basally, translucent distally; posterior lobe with a ragged (sometimes double) row of 5 to 7 stout spines.

Head with a distinct "neck," narrowed behind eyes. Eyes extremely large, globose, exserted, far removed from pronotum, without spines or visible setae; ocelli small, set on a tall slender tubercle. Bucculae platelike, protruding anteriorly, angulate; postclypeus bulbous, protruding anteriorly. First visible (second) rostral segment with 4 (2+2) stout spines directed ventrally (dorsally in repose), first pair at basal ¼, the second pair just past middle; second visible (third) rostral segment with several short setae. Head ventrally with 6 (3+3) long stout ventrally directed spines arranged in two longitudinal rows, one beneath each eye. Anterior acetabula set with a stout anteriorly directed spine. Anterior legs stoutest; anterior femur stout, tapering, ventrally set with two closely set longitudinal rows of short stout spines along with several long slender spines, 2 in anterior row and 3 in posterior row; anterior tibia beneath with a closely set row of distally angled stiff spine-like setae. Middle and hind legs slender, unarmed, with short setae. All tarsi long, slender, three segmented. Antennal segment 1 short and stout, 2 much longer and slender, 3 and 4 filamentary and extremely long.

Pronotum long, narrowed ahead of humeri, strongly constricted on anterior ⅔, expanded laterally on posterior ⅓; collar flared but not set off; callus raised, set with spines, weakly sulcate medially. Posterior lobe tumid, spinose, humeri prominent; posterior margin almost straight, with a weak posteriorly produced median angle. Scutellum raised, tapering to a sharp point posteriorly; with 2 (1+1) basal knobs laterally, with 2 to 4 stout spines on distal part, not always symmetrically placed; medially with a large oval depression.

Hemelytra elongate, membrane with four cells, inner cell longest; venation as in figure 6; hypocostal lamina well developed, foveate, widest behind metepisternum, tapering posteriorly, reaching nearly to membrane; except for membrane, covered with scattered stout spines, always placed on prominent veins.

Nymph not known.

Discussion. Erianotoides appears close to *Erianotus,* as the name implies but, according to a recently completed cladistic analysis (JTP, unpublished), is more

closely related to *Valleriola.* Apomorphies for *Erianotoides* are as follows: pattern of fore tibial spines (unique); isolated row of spines on posterior pronotal lobe (unique); tall slender ocellar tubercle (shared with *Erianotus*).

The smallest species of *Valleriola* (*wilsonae* Drake and *tribulosa* J.& D. Polhemus, both from Australia), share some key characteristics with *Erianotoides,* e.g., head as wide as pronotum due to the relatively large eyes, latter with dorsal setiform spines. The very thick conical spines on the pronotum, the second row of stout spines on the posterior lobe of the pronotum, the scattered stout spines on the hemelytra, the light coloration and the extremely long antennae immediately separate *Erianotoides* from any known species of *Valleriola,* and any other genus of Leptopodidae. (We have examined 22 species of *Valleriola* in comparison, 8 of them undescribed; all are dark in coloration.) These characters also separate *Erianotoides* from *Erianotus* and *Martiniola,* but in addition the spiny armature of the fore tibia of these genera is different, as given in the key.

Type-species. Erianotoides oculatus, new species.

Etymology. The name *Erianotoides* (masculine) refers to the similarity to *Erianotus.*

Distribution. Madagascar, Tulear Prov.

Erianotoides oculatus, new species

Figs. 1, 6–10; map 1

Description. See generic description. Head width/length 0.90/0.57, tan, shining, frons flat, nearly vertical, tylus prominent; eye width/length 0.27/0.47; frons covered with numerous very short recumbent golden setae; vertex depressed, bearing irregular brown patches to either side of midline adjoining inner margins of eyes; head separated from remainder of head by broad transverse sulcus, this sulcus pale tan centrally, marked with dark brown laterally; antennal segments I–III pale tan, lacking apparent setae except for a few semi-erect pale setae near tip of III, segment IV brown, covered with long semi-erect pale setae, lengths of segments I–IV: 0.27, 0.70, 2.33, 1.20.

Pronotum width/length 0.77/0.73; anterior margins slightly flared to form narrow collar set off by a transverse row of punctations; posterior lobe separated from anterior lobe by broad transverse depression, with a transverse row of 4–5 short sharp black spines near posterior margin; general coloration of pronotum pale tan, with irregular brown glabrous areas surrounding bases of calli and adjoining lateral margins, lateral and posterolateral margins raised to form narrow glabrous lip. Scutellum tan with basal angles dark brown, width/length 0.30/0.33; central portion with a semicircular depression, lateral areas around this depression slightly raised and rounded, bearing 2 (1+1) short sharp spines medially; basal angles each with a small rounded protruding dark tubercle; posteriorly elongate and acute.

Hemelytra tan with irregular brown fasciae, these fasciae variable in size and intensity, occupying the following areas: basal ¼ of corium and onto basal ⅓ of clavus, central portion of corium adjoining distal ⅓ of clavus, posterior part of corium adjacent to membrane; membrane pallid, length of clavus along outside margin 1.23, along commissure 0.90.

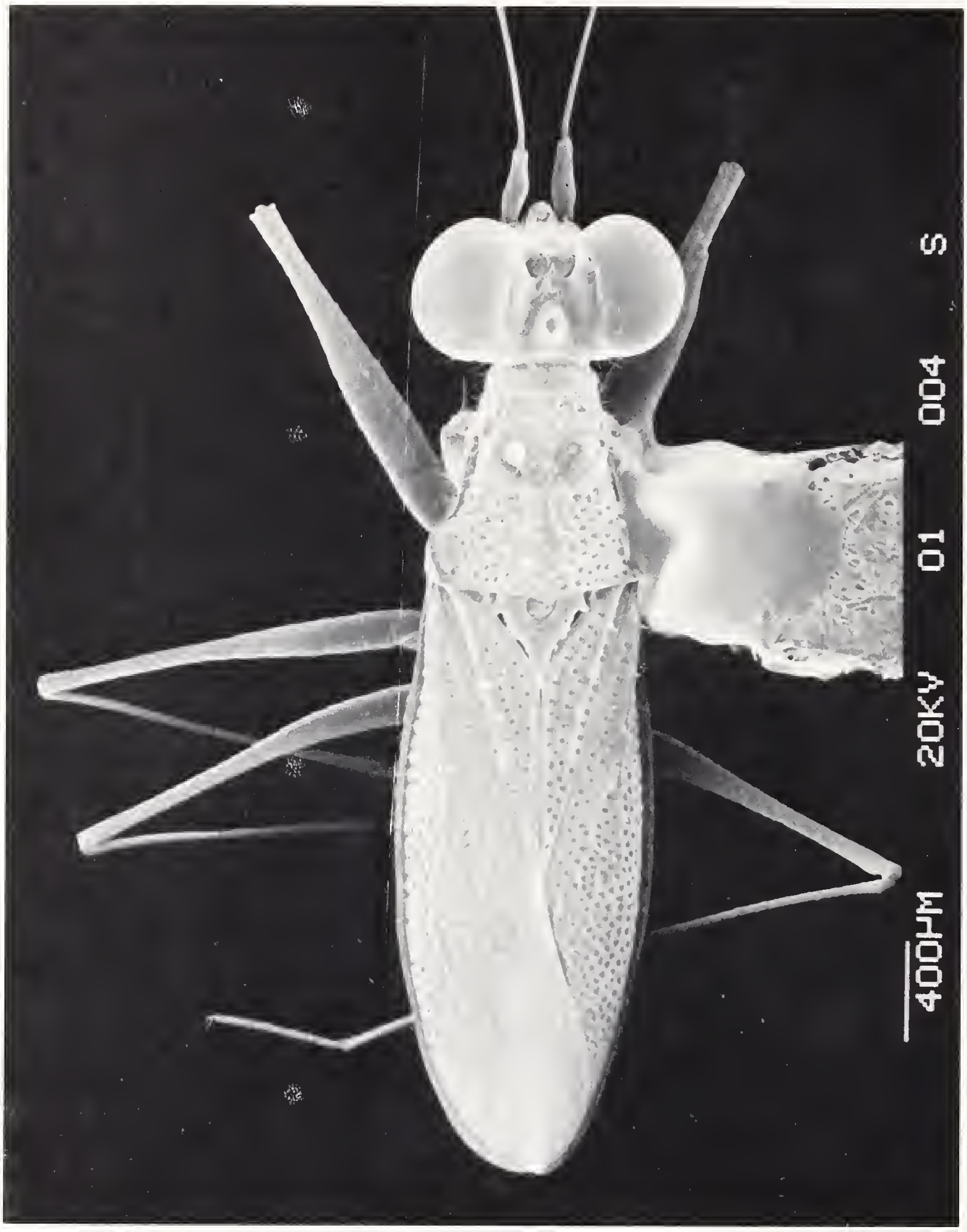

Fig. 1 *Erianotoides oculatus,* habitus.

Ventral surface of head, thorax, and abdomen tan, sparsely set with long slender semi-erect pallid setae; rostrum pallid, tip brown, sharply bent between first and second joint, length 0.80, attaining fore coxae in typical reflexed position. Legs elongate, slender, pallid, sparingly and irregularly marked with brown; fore- and middle femora with 4–6 raised brown patches on medial portion of posterior face; all leg

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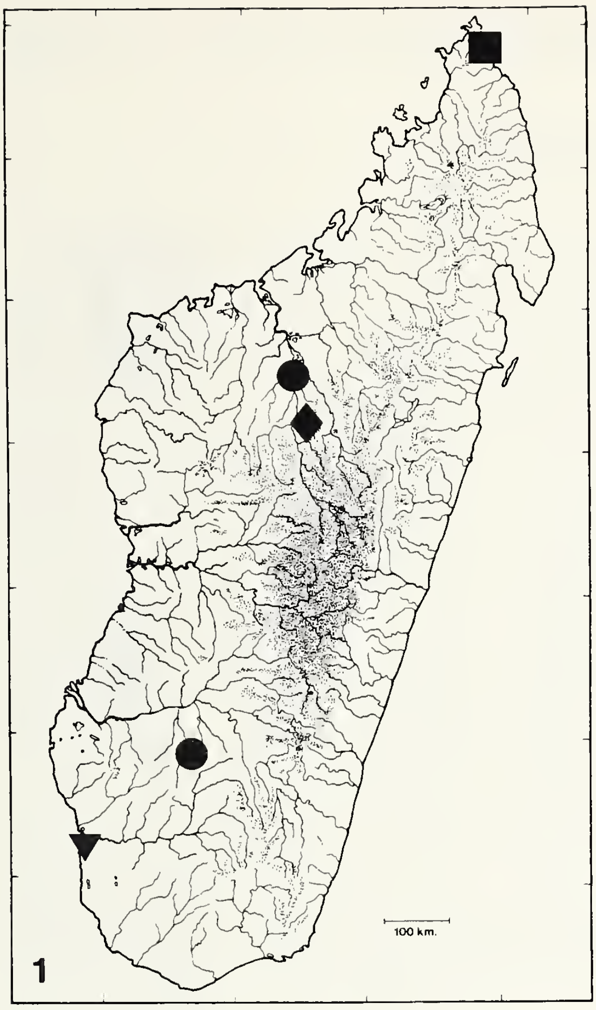
Map 1. Leptopodidae, distribution on Madagascar: *Erianotoides oculatus,* triangle; *Leptopoides horvathi,* square; *Martiniola madagascariensis,* circles; *Martiniola pulla,* diamond.

Map 2. Leptopodidae, distribution on Madagascar: *Valleriola strigipes.*

Map 3. Saldidae, distribution on Madagascar: *Rupisaldula slateri,* squares; *Rupisaldula vincenti,* circles; *Salduncula seychellensis,* diamond.

Map 4. Saldidae, distribution on Madagascar: *Saldula ornatula,* square; *Saldula niveolimbata,* diamond; *Saldula madagascariensis,* circles; *Capitonisaldoida cryptica,* triangle.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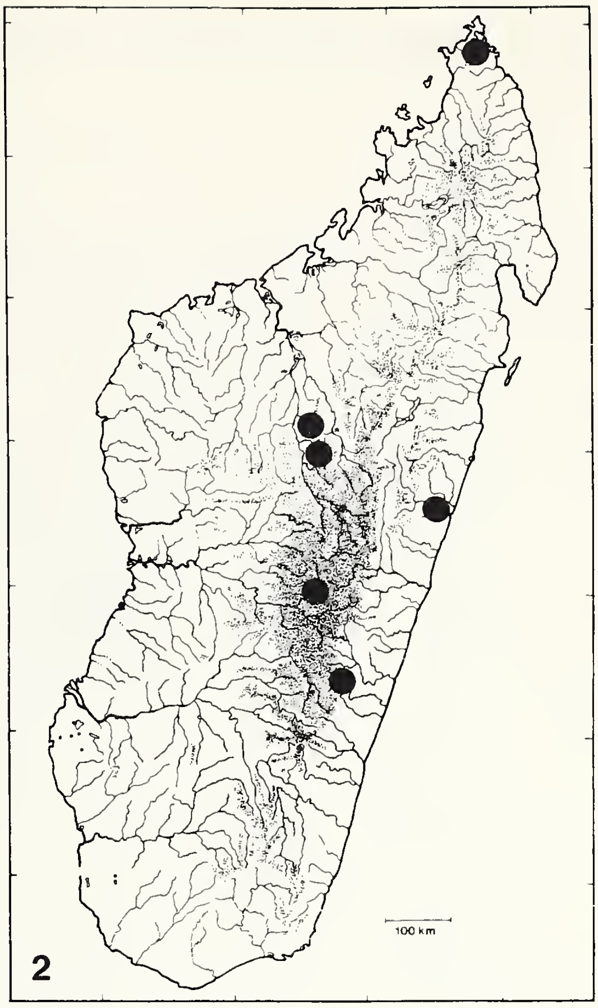
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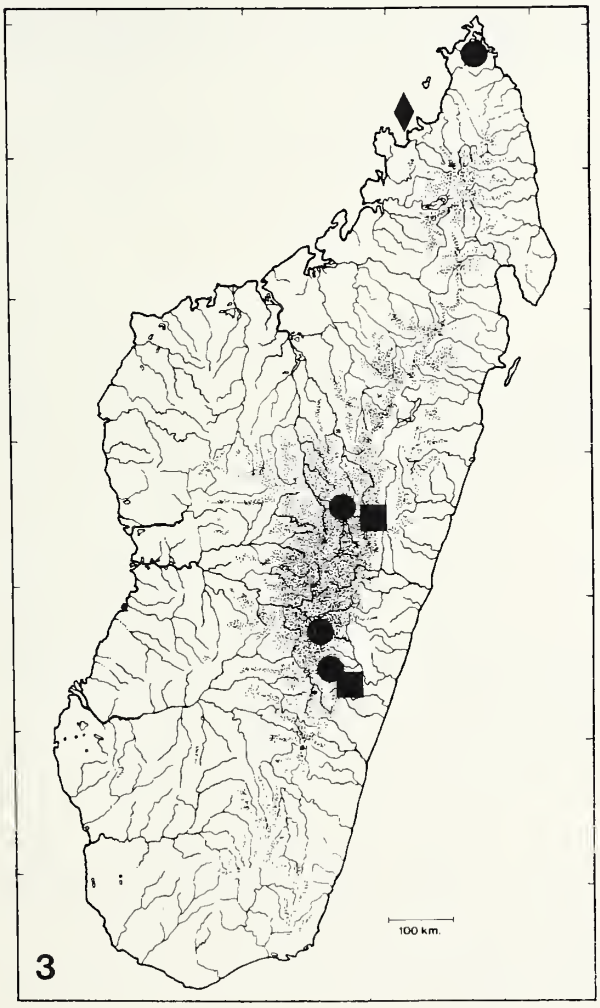
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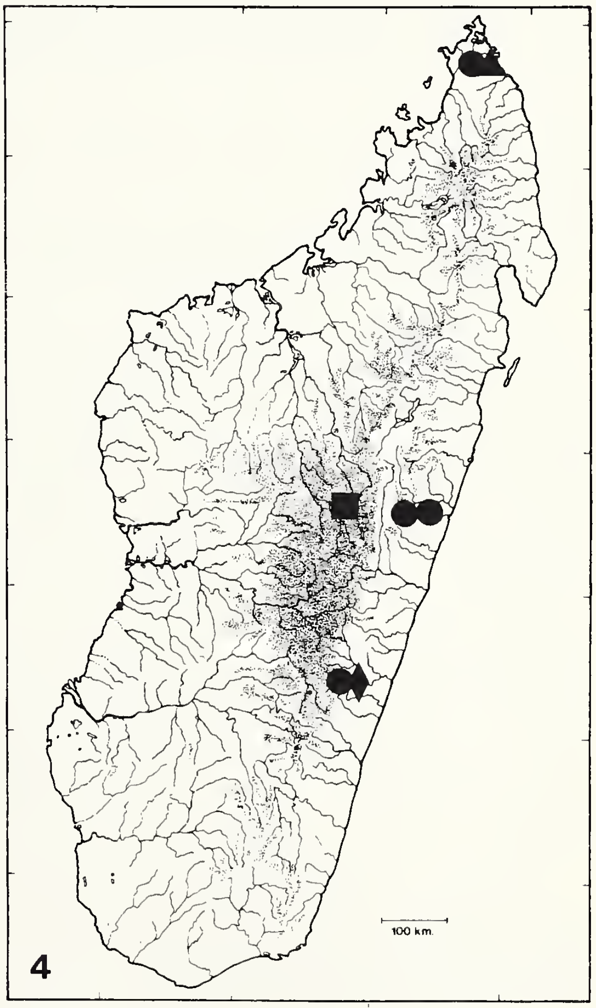
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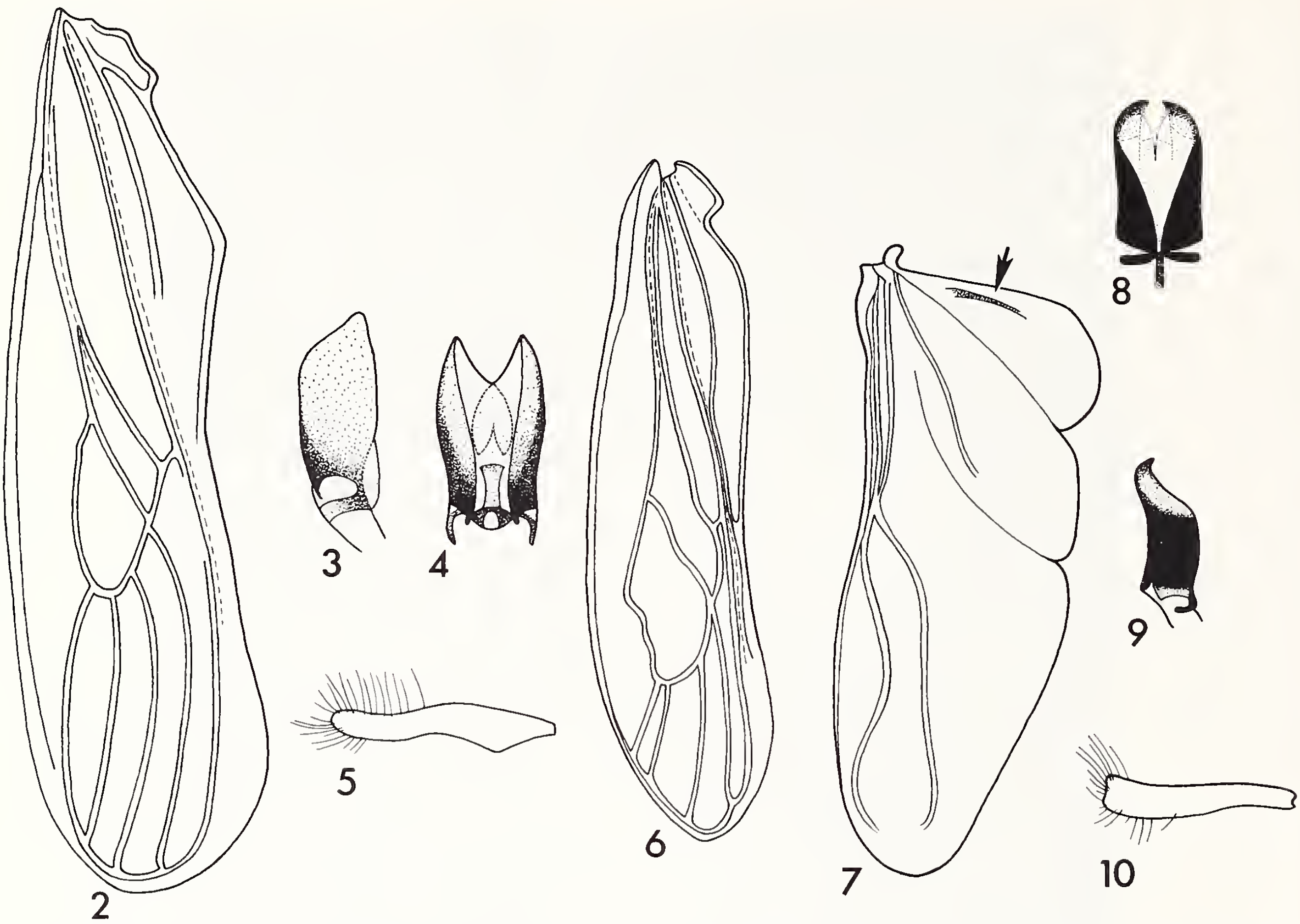


Figs. 2–10. Leptopodidae. 2–5. *Leptopoides horvathi.* 2. Hemelytra. 3–4. Male aedeagus, two views. 5. Male paramere. 6–10. *Erianotoides oculatus.* 6. Hemelytra. 7. Hind wing, showing vannus with stridulatory denticles (arrow). 8–9. Male aedeagus, two views. 10. male paramere.

segments covered with short recumbent golden setae; claws slender, gently curving, golden.

Male genitalia as in Figures 8–10.

Discussion. See under generic description.

Habitat data. Known so far only from Le Grotte, a limestone sink hole adjacent to the sea south of Tulear. This grotto contains a large pool fed by submerged fresh water springs, scattered with huge blocks of fallen limestone, some emergent. At high tide the pool is flooded by sea water and the surface level rises several feet. The humidity in this grotto remains fairly high and the air temperature quite moderate in spite of the dry searing heat in the spiny desert just above. The walls and ceiling of the grotto range from well lit to quite dark in the inner recesses. *E. oculatus* was collected from steep walls and the ceiling in the moderately well lit portions of the grotto, but not in direct sunlight; individuals ran rapidly over the surface and flew when disturbed. Because the bugs were the same color as the substrate they lived on they appeared ghost-like against the dimly lit rock.

Etymology. The name *oculatus* refers to the extremely large eyes in relation to the body.

Holotype. Macropterous male: MADAGASCAR, Tulear Prov.: Le Grotte, ~20km S of Tulear on St. Augustine Rd., sea level, CL 2293, XI-28-1986, J. T. & D. A. Polhemus (USNM).

Paratypes. 19 males, 14 females, same data as holotype (JTPC).

Leptopoides, new genus
Figs. 2–5

Description. Length 3.66 to 4.28 mm., width across hemelytra 1.03 to 1.26 mm. Ground color blackish brown, marked with testaceous to leucine; venter mostly dark in males except prosternum; in females abdominal venter leucine tinged with brown. Head thickly clothed with appressed pale pubescence; pronotum, hemelytra with pale scalelike setae; venter with short to moderate length pale setae. Dorsum faintly shining; pronotum except for calli, hemelytra except for membrane covered with closely set foveae, weaker on hemelytra. Dorsal surface without spines. Scutellum with 2 (1+1) basal knobs laterally. Eyes with scattered short slender setae.

Head with a distinct "neck," narrowed behind eyes. Eyes extremely large, globose, exserted, far removed from pronotum; ocelli small, set on a raised tubercle. Bucculae plate-like, protruding ventrally, angulate; postclypeus tumid, slightly protruding anteriorly. First visible (second) rostral segment with 4 (2+2) stout spines directed ventrally (dorsally in repose), first pair at basal ¼, the second pair just past middle; second visible (third) rostral segment with 4 (2+2) spines, first pair stout, second pair slender, and several stout setae. Head ventrally with 6 (3+3) long stout ventrally directed spines arranged in two longitudinal rows, one beneath each eye. Anterior acetabula set with a stout anteriorly directed spine; an adjacent spine arising from prosternum laterally behind collar. Forelegs stoutest; coxae medially set with a stout anteriorly directed spine, and distally with 2 distally directed spines; trochanter set with 6 ventrally directed spines; femur stout, tapering, ventrally set with two longitudinal rows of stout spines, 5 very long stout spines evenly spaced among 12–14 short spines in anterior row, and about 14 short spines in posterior row, along with 3 anteriorly directed long stout spines on anterior face; tibia beneath with a closely set row of distally angled stiff spines as long as width of tibia, and two long stout anteriorly directed spines on basal half. Middle and hind legs slender, unarmed, with short setae. All tarsi long, slender, three segmented. Antennal segment 1 short and stout, 2 much longer and slender, 3 and 4 filamentary and extremely long, distal segment set with recumbent setae.

Pronotum long, narrowed ahead of humeri; collar flared, set off by a row of pits; callus raised, weakly sulcate medially. Posterior lobe tumid, humeri prominent; posterior margin almost straight. Scutellum raised basally, depressed medially, roughly triangular; medially with a large rectangular depression set with 2 (1+1) tiny tubercles.

Hemelytra elongate, membrane with 4 cells, inner cell longest; venation as in Figure 2; lateral cell leathery, alveolate, similar to outer corium; hypocostal lamina well developed, foveate, widest behind metepisternum, tapering posteriorly, reaching nearly to membrane.

Nymph with complement of spines as in adult, but additionally with the following: spines on postclypeus, frons, vertex, eyes, pronotum, wing pads, all abdominal tergites and last two ventrites, middle acetabulae and coxae, middle and hind femora, a third long stout spine on anterior tibia, and 8 (4+4) spines on second visible rostral segment. With a single large median scent gland opening on posterior margin of third abdominal tergite.

Discussion. Leptopoides is very close to *Leptopus,* as the name implies, but may be separated from the latter by the relatively shorter second antennal segment (Ratio II/I, 1.79 to 2.00 in *Leptopoides,* 2.63 to 3.00 in *Leptopus*), the lack of spines on the

dorsum (However in *Leptopus travancorensis* Distant the dorsal spines are short to medium length, setiform, recumbent), the different forewing venation, and the arrangement of spines on the fore tibia; the latter is unique and an apormorphy.

Drake and Hottes (1951) mentioned the lack of dorsal spines and described the membrane cells, but in the unique type specimen the distal three antennal segments were missing. On the basis of the armature of the fore legs, spinose and flattened second rostral segment and venation of the hemelytra they placed *horvathi* in *Leptopus,* however in our view the venation of the hemelytra is an apomorphy (shared with *Valleriola*) and a key character separating the two genera. Compare the configuration of the membrane cells shown in Figure 2 with those of *Leptopus* shown in figure 21B, Polhemus 1985 (p. 47) where the lateral cell of the membrane is displaced distally.

This genus is the sister group of the *Leptopus* species occurring in India and nearby regions, a group typified by *Leptopus travancorensis* Distant. While the two genera may be separated by the characters given above, they are convergent in general appearance, leading Drake to misidentify a specimen of the latter species as *L. horvathi.* We have seen several closely related undescribed species of *Leptopus* from India.

Type-species. Leptopus horvathi Drake and Hottes 1951.

Etymology. The name *Leptopoides* (masculine) refers to the similarity to *Leptopus.*

Distribution. Madagascar, Comores.

Leptopoides horvathi (Drake and Hottes),
New Combination
Figs. 2–5; map 1

Leptopus horvathi Drake and Hottes, 1951. J. Kansas Entomol. Soc. 24:24. Type, male, Tealo, Madagascar, in Muséum National d'Histoire Naturelle, Paris.

Additional description. See generic description; only additional details given here. Coloration: Head with large quadrate spot behind ocelli, entire dorsum anterad of vertex and venter, leucine. Pronotum with narrow light stripe on lateral margins along most of length, posterior lobe with median longitudinal carina and two (1+1) large fascia removed from midline, yellowish. Hemelytra with embolium, all veins in or bordering clavus, basal angle of inner corium, medial and distal spots at outer edge of inner corium, 2 distal spots on outer corium, basal spot on membrane cell 1, leucine. Legs, basal part of antennae leucine to testaceous, antennae dark distally.

Female length 4.28, width 1.26. Head width 1.04; length 0.59; minimum interocular space 0.22; eye length 0.52, width 0.44. Length visible rostral segments I–III; 0.59, 0.33, 0.18. Length antennal segments I–IV: 0.22, 0.37, 1.15, 1.11. Pronotum length 0.81; width across humeri 1.00, across collar 0.48. Scutellum length (visible) 0.41; width 0.59. Hemelytra length 2.44; length claval commissure 0.67. Length of legs: anterior femur 1.37, tibia 1.04, tarsi (combined tarsal segments) 0.33; middle femur 1.44, tibia 1.55, tarsi 0.41; hind femur 1.55, tibia 2.18, tarsi 0.48.

Discussion. See key, generic description and discussion under *L. poissoni* below.

Habitat data. This species was found at only one locality near Diego Suarez, where it frequented medium sized rocks along a small partially shaded stream located in a small valley amid secondary dry deciduous forest. These insects ran rapidly over the

rock surfaces and flew with little provocation, necessitating quick work with an aspirator to capture them.

Material examined. MADAGASCAR, Diego Suarez Prov.: 36 males, 19 females, 7 nymphs, small forest stream 5 km N of Joffreyville, 488 m, CL 2281, Water temp. 20°C, XI-16-1986, J. T. & D. A. Polhemus (JTP).

Leptopoides poissoni, new species

Description. See generic description; only additional details given here. Coloration: Head with large quadrate spot behind ocelli, entire dorsum anterad of vertex and venter, leucine. Pronotum with short narrow light stripe on lateral margins ahead of humeri, median longitudinal carina on posterior lobe, yellowish. Hemelytra with embolium, all veins in or bordering clavus, medial spot at outer edge of inner corium, basal spots on membrane cells 1 and 2, leucine. Legs, antennae leucine to testaceous. Female length 4.28, width 1.26. Head width 1.11; length 0.67; minimum interocular space 0.22; eye length 0.52, width 0.44. Length visible rostral segments I–III: 0.48, 0.30, 0.18. Length antennal segments I–IV: 0.26, 0.52, 1.30, 1.52. Pronotum length 0.93: width across humeri 1.15, across collar 0.48. Scutellum length (visible) 0.41; width 0.56. Hemelytra length 2.81; length claval commissure 0.67. Length of legs; anterior femur 1.37; tibia 1.07, tarsi (combined tarsal segments) 0.37; middle femur 1.52, tibia 1.59, tarsi 0.44; hind femur 1.59, tibia 2.37, tarsi 0.41.

Discussion. The unique female is very similar to *L. horvathi* in general appearance, but differs in having the third antennal segment relatively shorter than the fourth (III:IV; 1.30:1.52 vs. 1.15:1.11 in *horvathi*) and much shorter spines on the anterior femora (longest spine length:max. width of anterior femur; 0.18:0.18 vs. 0.36:0.18 in *horvathi*).

Habitat data. Not known.

Etymology. Named for Raymond Poisson to recognize his contributions to the study of the aquatic Heteroptera of Madagascar and the African region.

Holotype. Macropterous female, COMORES ISL., Moheli: Environs Cascade Kangani, VI-1954, J. M. (CJD, Poisson Coll.).

KEY TO THE SPECIES OF *MARTINIOLA*

1a. Ground color brownish black, sparsely marked with testaceous or leucine. Ratio of antennal segments II–IV: 1.19, 1.44, 0.83 .... *pulla* Drake

1b. Ground color yellowish brown to dark brown, more extensively marked with testaceous or leucine. Ration of antennal segments II–IV: 1.19, 1.22, 0.65 .... *madagascariensis* (Martin)

Martiniola madagascariensis (Martin)
Map 1

Erianotus madagascariensis Martin, 1897. Bull. Soc. Entomol. Fr. 1897:274. Types, 2 specimens (sex not known), Madagascar, in Muséum National d'Histoire Naturelle, Paris.

Martiniola madagascariensis Horvath, 1911. Ann. Mus. Nat. Hung. 9:366, fig. 3.

Discussion. We did not collect this species, but we have studied material in the

Drake Collection (CJD) and the Polhemus Collection (JTPC). The coloration of this species is quite variable in a given series, and the structural characteristics are almost identical to *M. pulla* Drake. Only the antennal ratios separate the two species, and as only one specimen of each was available with the antennae entire, and these were of opposite sexes, this character may prove to be sexually dimorphic or variable. When a series of *pulla* including males becomes available we suspect that it may prove to be only a dark color form of *madagascariensis.*

Material examined. MADAGASCAR, Tulear Prov.: 3 males, 1 female, Isalo, Coll. R. P. [Paulian?], VIII-41 (CJD, JTPC): Majunga Prov.: 1 male, 1 female, Maevatenana, VIII-41, collector's name illegible (CJD).

Martiniola pulla Drake
Map 1

Martiniola pulla Drake, 1955. Proc. Biol. Soc. Wash. 68:110. Type, female, Tamatave, Madagascar, in C. J. Drake Collection, USNM.

Discussion. See under *M. madagascariensis* (Martin). Our single specimen was collected along with *Valleriola strigipes* on natural stone walls and large boulders along the Mamokomita River.

Material examined. MADAGASCAR, Majunga Prov.: 1 female, Mamokomita River and tributaries, 19 km SE of Andriba, 655 m, CL 2270, XI-8-1986, J. T. & D. A. Polhemus (JTP).

Valleriola strigipes (Bergroth)
Figs. 11–14; map 2

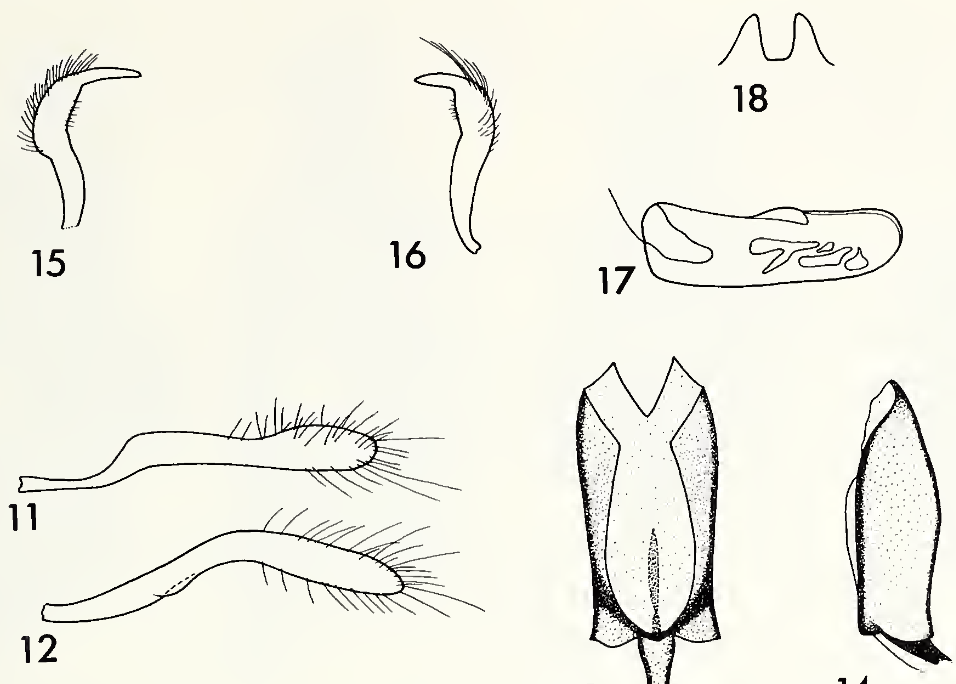
Leptopus strigipes Bergroth, 1892. Ann. Entomol. Soc. Fr. 60 (Bull.): CLI. Types, 2 specimens, sex unknown, Madagascar, in Muséum National d'Histoire Naturelle, Paris.

Valleriola strigipes Horvath, 1911. Ann. Mus. Nat. Hung.: 364.

Discussion. This is a common widespread species in Madagascar, and is easily separated from its African congeners by the hairy dorsal vestiture and distinctive light markings. These insects generally favor steeply sloping rock or cement walls just above the water surface of streams or ponds, although some specimens were taken quite removed from the water. Due to its preference for such open vertical substrates shielded from direct sunlight this species is often found on bridge abutments.

Bergroth (1892) described this species as a *Leptopus* species, and in 1906 again placed it in *Leptopus* and maintained that *Valleriola* was a synonym of the latter. Horvath (1911) showed that *Valleriola* was a distinct genus and placed *strigipes* in it.

Material examined (all collected by J. T. & D. A. Polhemus, all in JTPC). MADAGASCAR, Diego Suarez Prov.: 3 males, 3 females, rocky river and waterfall, 43 km S of Diego Suarez, 91 m, CL 2275, XI-12-1986. Majunga Prov.: 1 male, 1 female, Mamokamita River and tributaries, 19 km SE of Andriba, 655 m, CL 2270, XI-8-1986. Fianarantsoa Prov.: 2 females, 1 nymph, Tamara Creek at Ambatolahy, 4.5



Figs. 11–18. Leptopodidae, Saldidae. 11–14. *Valleriola strigipes.* 11–12. Male paramere, two views. 13–14. Male aedeagus, two views. 15. *Salduncula seychellensis,* male paramere. 16–18. *Saldula madagascariensis.* 16. Male paramere. 17. Aedeagus. 18. Parandria.

km W of Ranomafana, 885 m, CL 2251, X-31-1986. Tamatave Prov.: 4 males, 9 females, stream W of Antsampanana, 32 km S of Brickaville, 46 m, CL 2259, XI-4-1986. Tananarive Prov.: 5 males, 4 females, waterfalls and rapids, 61 km N of Ambositra, 1,387 m, CL 2242, X-29-1986; 1 male, Manakazo River at Manakazo Forest Station, 1,417 m, CL 2267, XI-7-1986.

FAMILY OMANIIDAE

The family Omaniidae is represented on the islands of the western Indian Ocean region by two species. One of these, *Corallocoris aldabrae* (Cobben, 1987b), was recently described from Aldabra and is discussed below. The other, *Omania coleoptrata,* is known from the coasts of the Red Sea, Oman, and Pakistan, all outside of the region treated here.

Corallocoris aldabrae Cobben

Corallocoris aldabrae Cobben, 1987. Revue Zool. Afr. 101:24. Type, female, Aldabra, Middle Island near East Channel, in British Museum (Natural History), London.

Discussion. This species was described from a single mutilated female, said to differ from *Corallocoris marksae* (Woodward) by the larger frontal light spots on the frons, lighter first acetabulae, and clearly notched hypocostal lamina of the forewing.

On Aldabra Atoll this species has been taken only along the margins of Passe Houareau, the easternmost of the channels connecting the lagoon to the open ocean. The insects were found here under and amid rounded coral cobbles lying on a bed of firm sand at the high tide line. For a further discussion of the habitat and behavior of *C. aldabrae* at Aldabra see D. Polhemus (1990).

Material examined. ALDABRA ATOLL, Malabar Is.: 27 adults, 8 immatures, shore of limestone and coral cobbles just north of Middle Camp, western side of Passe Houareau, low tide, 1300 hr, 22 March 1989, CL 8036, D. A. Polhemus (USNM, JTPC).

FAMILY SALDIDAE

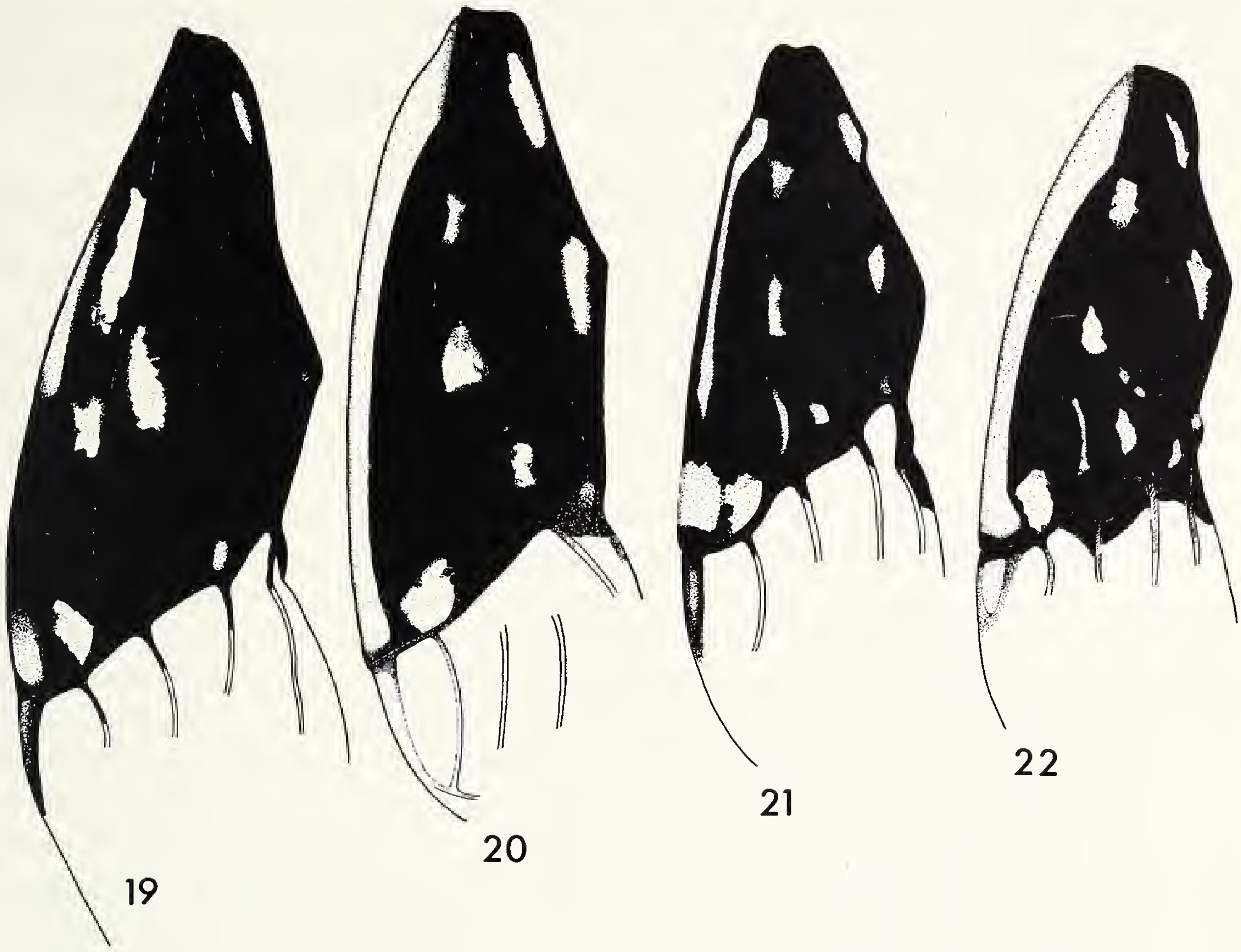
Paulian (1961) noted that 3 species of shore bugs were known from Madagascar, but did not list them. Cobben (1987a) briefly reviewed the Saldidae of Madagascar and added one new species. He also noted another undescribed species that he did not name due to the poor condition of the specimen; it is a large species (6.5 mm) and does not seem to be any of those that we have studied.

KEY TO THE GENERA OF SALDIDAE OF MADAGASCAR, THE COMORES AND MASCARENES
(For terminology see J. Polhemus 1985)

1a. Transverse swelling of frons absent; pronotum short, length of head equal to or greater than 1.5 times the length of pronotum on midline .... *Salduncula* Brown
1b. Transverse swelling of frons present; pronotum long, length of head less than 1.5 times the length of pronotum on midline 2
2a. Hypocostal ridge produced ventrally into a laminar structure; anterior pair of facial trichobothria reduced or absent .... *Mascarenisalda* n. gen.
2b. Hypocostal ridge simple or with secondary ridge, but not produced ventrally into a laminar structure; anterior pair of facial trichobothria present 3
3a. Secondary hypocostal ridge present .... *Saldula* Van Duzee
3b. Secondary hypocostal ridge absent 4
4a. Ratio eye width/minimum interocular space, 0.86; hind tarsal segment 2 ventrally set with 6 stout spines in posterior row, distal spine only slightly longer than others; tarsal segment 3 ventrally set with 6–7 stout spines in the posterior row plus several moderate length setae distally but without a very long setae arising at distal ¾. Ocelli separated by more than the width of an ocellus .... *Capitonisaldoida* n. gen.
4b. Ratio eye width/minimum interocular space, 1.05 to 1.25; hind tarsal segment 2 ventrally set with 3–5 stout spines in the posterior row, distal spine about 2× longer than any other; tarsal segment 3 ventrally set with 1–2 stout spines in posterior row plus a single setae much longer than the spines arising at distal ¾. Ocelli approximate, separated by about ½ the width of an ocellus .... *Rupisalda* Polhemus

Capitonisaldoida, new genus
Figs. 19, 23–27, 42–43, 46–47

Description. Of moderate size, ovate, length 4.6 to 5.6 mm, width across hemelytra 1.9 to 2.3 mm; sexes dimorphic in size, males noticeably smaller. Ground color shining blackish brown, marked with testaceous to leucine; venter mostly dark in males; in females abdominal venter brown tinged with leucine; pronotal margins yellowish at least on posterior half; light markings on clavus and corium evident. Head with frons faintly rugulose, vertex smooth; broad, width 73 to 77% of greatest pronotal width. Head, pronotum, hemelytra clothed with fine dark medium length



Figs. 19–22. Saldidae, hemelytra. 19. *Capitonisaldoida cryptica*. 20. *Rupisalda atra*, n. sp. 21. *R. slateri*. 22. *R. vincenti*. (hairy vestiture not shown).

setae and very fine golden recumbent pubescence; venter with short to moderate length pale setae; legs with scattered short slender setae and usual spines. Antennae long, slender, with short recumbent pubescence and scattered longer setae, some longer than the segment where they arise.

Eyes not appressed to thorax, large, globose, exserted, distinctly removed from pronotum; ocelli small, not raised, separated by the width of an ocellus; postclypeus not tumid, not sulcate longitudinally; transverse swelling weakly developed.

Pronotum short, about ¾ as long as head on midline, anteriorly narrowed, margins weakly concave; collar narrow, set of by a weak row of pats; callus raised, median pit well developed, set off from broadly convex posterior lobe by a weak curving row of pits (largely hidden by pubescence) not reaching lateral pronotal margins. Scutellum wider than long; medially with a weak transverse sulcus. Posterior tibial comb absent; hind tarsal segment 2 ventrally set with 6 stout spines in posterior row, distal spine only slightly longer than others; tarsal segment 3 ventrally set with 6–7 stout spines in the posterior row plus several moderate length setae distally but without a very long setae arising at distal ¾. No stridulatory mechanism evident.

Hemelytra elongate, lateral margins almost straight basally, evenly convex distally, macropterous; embolar fracture present, typical of Saldinae; embolar modification of female not evident dorsally; venation of corium weakly indicated; membrane long, well developed, with four cells, inner cell much shorter than adjacent cell; hemelytra

as in Figure 19: hypocostal ridge simple, well developed but not strongly produced ventrally, more pronounced posteriorly in females; secondary hypocostal ridge absent; female costal margin slightly reflexed medially; hind wings well developed, reaching beyond apex of abdomen.

Eversible abdominal gland present. Female with 7 ovarioles; second gonapophysis truncate apically, not sharp (Fig. 27); connecting piece of styloids attached basally; ring gland of gynatrium plainly sclerotized; spermatheca with single distal pump flange. Male filum gonopori coiled one and two-thirds times; processus sensualis of paramere very weakly developed, indistinct (see Fig. 23).

Nymph. Larval organ present but small, not protuberant, located slightly mesad of spiracle on ventrite III; abdominal scent glands well developed, without lateral channels.

Discussion. Capitonisaldoida new genus appears very close to *Capitonisalda* Polhemus 1981, as the name implies. It lacks a secondary hypocostal ridge, however, and the ocelli are separated by more than the width of an ocellus (vs. at most the width of an ocellus in *Capitonisalda*). The preocellar spot in *Capitonisalda* is wedge-shaped and transverse, the narrow end of the wedge approaching or touching the ocelli, whereas in *Capitonisaldoida* the preocellar spot is elongate, usually forming a crescent with the anterior part paralleling or touching the eye and the posterior part curving medially toward but never touching the ocelli. In *Capitonisalda* the pronotal callus is not prominently raised and/or distinct from the posterior lobe, the frons of the head is smooth or at most has rather anteriorly situated weak tumescences on each side, whereas in *Capitonisaldoida* the pronotal callus is prominently raised and distinct, and the frons is smooth except for a distinct indentation medially set with a short broad longitudinal sulcus. The male genital structures also differ in these two taxa; the endosomal sheath of *Capitonisalda* has a narrow stem expanded and deeply cleft basally and lobed in the usual saldid manner (Figs. 44, 48), and the basal apicolateral endosomal sclerite is bifurcate basally, forming two stout lateral arms (the upper short in one undescribed species; see Figs. 44, 49), whereas in *Capitonisaldoida* the endosomal sheath has a broader parallel-sided stem, not expanded, only weakly cleft basally and not lobed (Figs. 42, 46), and the basal apicolateral endosomal sclerite not bifurcate basally, as shown in Figures 26, 42 and 47. These two apomorphies as well as the other key characters discussed above separate *Capitonisaldoida* from its congeners.

(Note: after the body of this paper was completed, several additional differences between *Capitonisaldoida* and Capitonisalda were called to our attention by Dr. Per Lindskog during his visit to our laboratory. These include features of the endosomal sheath, sclerites of the male genitalia, and the shape of the preocellar spots. He has generously shared some of his observations on the delineation of saldid genera and provided comparative photos and figures for inclusion here.)

Capitonisaldoida belongs to a circumtropical assemblage of saldid species from the New World, Australia, Africa, and Madagascar that live in the same microhabitat: dark recesses in very wet places such as vertical rock faces with gently sheeting water or waterfalls splash zones. All of these species have a broad interocular space and a similar general facies, but this is apparently convergence, since almost every zoogeographical region apparently has its own genera, not all in the same clade.

Type-species. Capitonisaldoida cryptica new species.

Etymology. The name *Capitonisaldoida* (feminine) refers to the similarity to *Capitonisalda.*

Distribution. Madagascar (Mt. D'Ambre).

Capitonisaldoida cryptica, new species
Figs. 19, 23–27, 42–43, 46–47; map 4

Description. Head width/length 1.37/0.73, black, with transverse dark yellow stripe running across frons above base of tylus, tylus brown; eye width/length 0.37/0.60; frons and vertex covered with numerous very short recumbent golden setae sparsely intermixed with a few longer erect golden setae on vertex; antennae slender, brown, lengths of segments I–IV: 0.43, 1.17, 0.73, 0.70.

Pronotum shining black, width/length (midline) 1.90/0.67; lateral margins weakly concave, narrowly bordered with dark yellow; posterior margin of posterior lobe broadly concave medially; surface of entire pronotum covered with very short recumbent golden setae. Scutellum black, shining, width/length 1.37/1.33; anterior lobe only weakly raised, bearing shallow semicircular depression medially along posterior margin; posterior lobe weakly convex; surface of both lobes covered with very short recumbent golden setae.

Hemelytra black, portion inside of radial vein dull, portion outside of radial vein shining; clavus length along outside margin 2.17, length of commisure 0.83, each side bearing a small elongate dark yellow spot basally along inner margin; corium with each side bearing 2 elongate dull white spots, one to inside of radial vein near middle of vein, another on anterior ⅓ of embolium outside of and adjoining radial vein, and 2 small roughly circular dull white spots, one along medial portion of posterior margin adjoining membrane, another at base of embolar fracture; embolar margin narrowly bordered with dark yellow, black on basal ⅙ and at extreme posterior end; wing membrane fumate, lateral margin with narrowly triangular thickened dark yellow area extending from base to near apex, veins darker; surface of clavus, corium emoblium and thickened membranal area bearing numerous short recumbent semi-erect golden setae.

Ventral surface of head, thorax, abdomen and hypocostal ridge black, posterior margins of abdominal ventrites often narrowly bordered with creamy white; female subgenital plate broadly white; rostrum brown, length 2.10, attaining bases of hind coxae; entire ventral surface covered with short fine recumbent golden setae. Legs predominantly yellowish brown, darker on dorsal surfaces; all leg segments covered with short recumbent golden setae sparsely intermixed with longer fine upright golden setae; scattered erect black spines present on fore, middle and hind tibiae; claws slender, gently curving, golden.

Male genitalia as in Figures 23–26.

Discussion. See under generic description above.

Habitat data. This species was found only in the spray and splash zone under the high main waterfall at Grande Cascade. Individuals occurred in dark recesses and pockets, usually on vertical or overhanging basalt faces protected from direct spray or wetting but still in a very moist environment.

Etymology. The name *cryptica* refers to the very secluded microhabitat in which this species lives.

Holotype. Macropterous male, MADAGASCAR, Diego Suarez Prov.: Mt. D'Ambre, Grande Cascade, 671 m, CL 2278, XI-13-1986, J. T. & D. A. Polhemus (USNM).
Paratypes. 17 males, 12 females, 12 nymphs, same data as holotype (JTPC,TSIM).

Mascarenisalda, new genus
Figs. 28–31

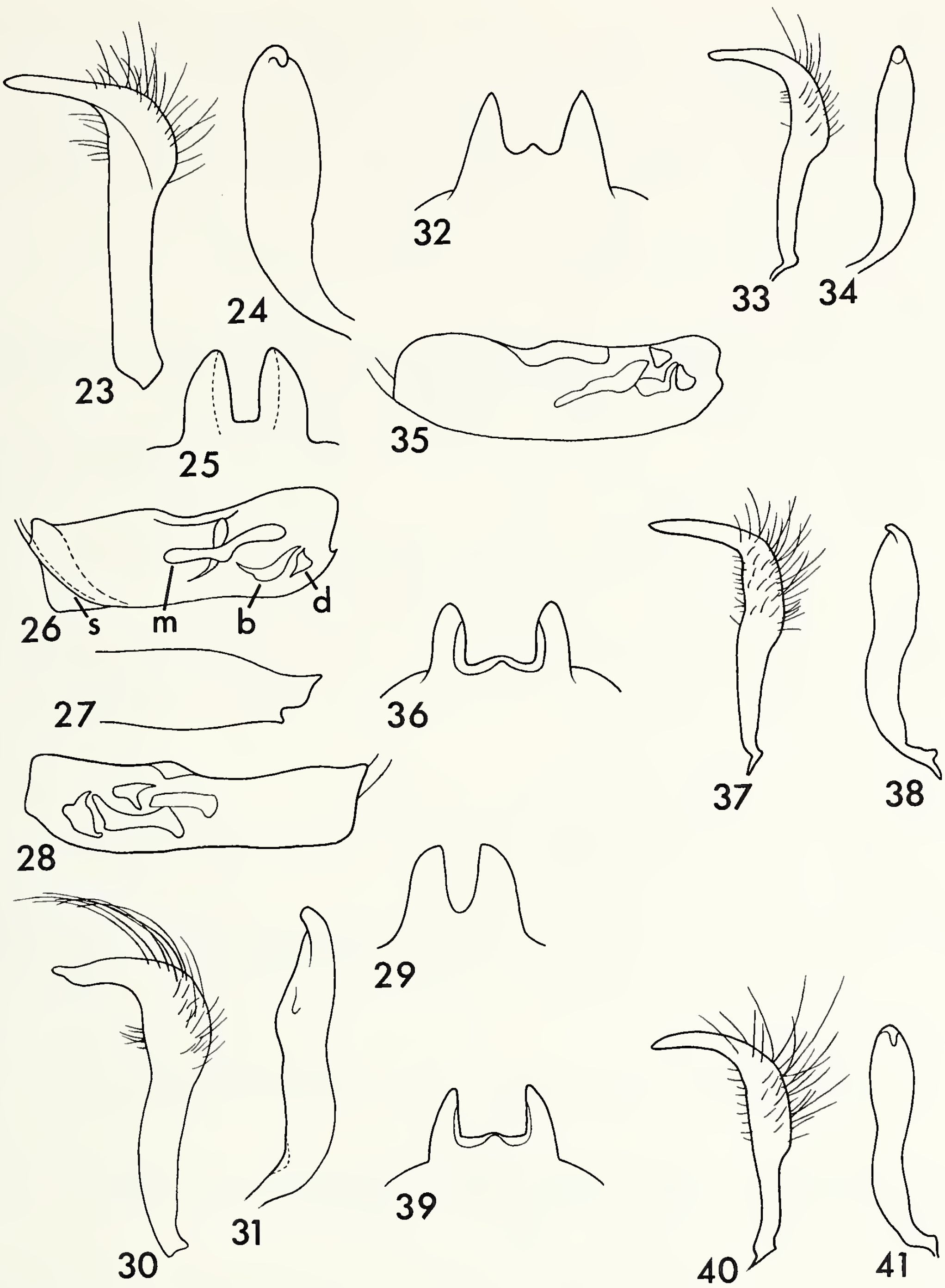
Description. Length 2.7 to 3.9 mm., width across hemelytra 1.4 to 1.8 mm. Ground color variable blackish brown to yellowish brown, extensively marked with testaceous, luteous, leucine, and white; venter usually luteous, abdomen medially mostly dark in males, lighter in females; pronotum with margins yellowish along most of length, variably marked with luteous, sometimes entirely luteous tinged with brown; light markings on clavus and corium extensive. Head with frons raised, sculptured, vertex smooth, broad, width 60% (macropterous female) to 86% (brachypterous male) of greatest pronotal width. Head, pronotum, scutellum clothed with coarse golden recumbent pubescence; hemelytra covered with dark medium length setae; venter with short recumbent pale setae; legs with scattered short slender setae and usual spines. Antennae long, slender, with short recumbent pubescence and scattered longer setae on distal 2 segments, not longer than the width of the segment of origin.

Head free from thorax, eyes large, globose, exserted, distinctly removed from pronotum; ocelli large, slightly raised, separated by less than the width of an ocellus; postclypeus tumid, sulcate longitudinally, flanked by 2 (1+1) additional tumescent ridges diverging anteriorly; transverse swelling strongly developed; with only the posterior two pairs of stiff black trichobothria evident instead of the usual three pairs.

Pronotum short, about as long as head on midline, strongly narrowed anteriorly, margins almost straight; collar wide, set off by a prominent row of pits; callus raised, median pit well developed, with broad median longitudinal sulcus, set off from posterior lobe by a prominent row of pits not reaching lateral pronotal margins. Scutellum about as wide as long; medially with a weak transverse sulcus. Posterior tibial comb present. No stridulatory mechanism evident at 80×, however it is possible that an SEM study will reveal extremely fine serrations on the sclerotized ventral margin of the hypocostal lamina.

Hemelytra truncate (brachypters) to elongate (macropters), lateral margins rather evenly convex in males, females with lateral (costal) margin slightly sinuate; brachypterous, submacropterous or macropterous; costal fracture present, typical of Saldinae; embolar modification of female evident dorsally as a short reflexed section; venation of corium weakly indicated; membrane variable, abbreviated to long with four cells, inner cell shorter than adjacent cell; hypocostal ridge consisting of a well developed lamina, strongly produced ventrally, with a sclerotized ventral margin, the entire lamina forming a shallow sulcus closed posteriorly at distal 5/6 (toward embolar fracture); secondary hypocostal ridge absent; female costal margin slightly reflexed at distal ⅔; hind wings reduced to well developed.

Eversible abdominal gland present. Female first gonapophysis with 10 stout teeth, weaker basally; second gonapophysis truncate apically, notched, not sharp; connecting piece of styloids free, not attached basally; ring gland of gynatrium weakly sclerotized; spermatheca with single distal pump flange; egg similar in shape to figure 1C in Cobben (1968:9). Male filum gonopori coiled two and one-half times; processus



Figs. 23–41. Saldidae, genitalic structures. 23–27. *Capitonisaldoida cryptica*. 23–24. Male paramere, two views. 25. Parandria. 26. Aedeagus: b, basal apicolateral sclerite; d, distal apicolateral sclerite; s, endosomal sheath; m, median endosomal sclerite. 27. Female second gonapophysis. 28–31. *Mascarenisalda mametiana*. 28. Aedeagus. 29. Parandria. 30–31. Male paramere, two views. 32–35. *Rupisalda atra*. 32. Parandria. 33–34. Male paramere, two views. 35. Aedeagus. 36–38. *R. slateri*. 36. Parandria. 37–38. Male paramere, two views. 39–41. *R. vincenti*. 39. Parandria. 40–41. Male paramere, two views.

sensualis of paramere very well developed, forming a sclerotized ridge (see Figs. 30–31).

Nymph. Head with 4 pairs of stiff cephalic setae. Wing pads almost entirely rugulose, covered with scale-like pads. Abdominal scent gland with two distinct slit-like openings, without lateral channels. Larval organ very large, raised, located almost at lateral edge of abdominal sternite 3.

Discussion. In Polhemus' cladistic analysis of the saldid genera of the world, this is 'genus C' (see J. Polhemus 1985:104). The apparent loss, or at least extreme reduction, of the anterior pair of cephalic trichobothria is a unique occurrence in the Leptopodomorpha as far as we know, and is an apomorphy. The laminar hypocostal ridge sets this genus apart from others occurring in the Indian Ocean region, but is convergent with several other genera from other parts of the world (e.g., St. Helena, the Palearctic region, and Hawaii). *Mascarenisalda* belongs to the same clade as an undescribed genus from Hawaii (placed in *Saldula* by Cobben, but far removed from the latter cladistically), but is separated from the Hawaiian genus by the extremely long setae arising from the corpus paramerus (see J. Polhemus 1985:100, apomorphic character 86), and the reduced anterior cepahalic trichobothria.

In one specimen there is a whitish waxlike substance in the channel-like lateral depression formed by the hypocostal lamina and costal margin, and also on the lateral part of the secondary scent fluid channel (formed by the episternal flap and metepisternum; for explanation, figures and terminology, see J. Polhemus 1985:29, figs. 16B–D). This coupled with the tight fit of the basal hypocostal region of the hemelytra and metepisternum suggests that the remarkably well developed hypocostal lamina functions as an extensive evaporatory surface for the fluids produced by the scent gland. The episternal flap in this species also has folds, which would increase surface area and tend to hold fluid.

Type-species. Saldula mametiana Drake 1953.

Etymology. The name refers to the restricted occurrence of this genus on the Mascarene island of Mauritius; feminine.

Distribution. As far as is known, this monotypic genus is restricted to Mauritius, although we have not collected on the nearby islands of Rodriguez and Reunion.

Mascarenisalda mametiana (Drake), **New Combination**
Figs. 28–31

Saldula mametiana Drake, 1953. Le Naturalist Malgache 5:167. Type, macropterous male, Mauritius, in C. J. Drake Collection, USNM.

Discussion. On Mauritius we found *Saldula mametiana* in a diverse array of microhabitats, which is characteristic of island species that are without competition; a similar situation prevails with *Saldula tahitiensis* Cobben on Tahiti. Brachypterous, submacropterous and macropterous forms with a wide range of total body sizes were commonly found together on mud and sand stream banks, vertical rock surfaces around waterfalls, seeping rock faces, mossy places, and bare surfaces on midstream rocks.

This species is quite highly marked with white and fulvous bands and spots, more so than Drake's habitus figure would indicate (see Drake, 1953, fig. 1); it is reminiscent of *Saldula opacula* Zetterstedt but more colorful than the latter.

Material examined (all collected by J. T. & D. A. Polhemus, all JTPC). MAURITIUS, Black River Dist.: 30 males, 26 females, 6 nymphs, stream 2 km S of Chamarel, 198 m, CL 2232, X-22-1986. Flacq Dist.: 1 male, 2 females, stream in cane field nr. Deep River, 150 m, CL 2226, X-20-1986. Moka Dist.: 20 males, 9 females, 3 nymphs, rocky mountain stream, 1 km E of Belle Rive, 573 m, CL 2225, X-20-1986. Plaines

Wilhelms Dist.: 28 males, 9 females, 3 nymphs, rocky stream at Curepipe, 500 m, CL 2222, X-19-1986. Savanne Dist.: 3 males, 3 females, 1 nymph, rocky stream nr. Grand Bassin, 579 m, CL 2229, X-21-1986; 5 males, 7 females, 1 nymph, rocky stream at viewpoint nr. Cascade Cecile, 625 m, CL 2231, X-21-1986. Also 1 male paratype, MAURITIUS, IV-14-1951, Ray Mamet (JTPC).

KEY TO THE SPECIES OF *RUPISALDA* OF MADAGASCAR AND THE COMORES

1a. Lateral margins of pronotum concolorous with disc, without light markings .. *atra*, n. sp.
1b. Lateral margins of pronotum each with a prominent yellowish longitudinal stripe ... 2
2a. Dorsum with long erect setae .... *vincenti*, n. sp.
2a. Dorsum without long erect setae .... *slateri*, n. sp.

Rupisalda atra, new species
Figs. 20, 32–35

Description. Large for genus, shape ovate, length 4.70–5.00 mm; maximum width (across hemelytra) 2.20–2.60 mm; ground color shining black, sparingly marked with white and dark yellow.

Head black, rugulose, width/length 1.15/0.59, bearing 2 (1+1) small yellow spots on upper frons at bases of trichobothria, 2 (1+1) additional wedge-shaped yellow spots present along inner eye margins on either side of vertex; ocelli large, yellowish; eyes large, protrusive, brown, width/length 0.30/0.48; frons and vertex covered with fine semi-recumbent golden setae; antennae slender, light brown, covered with short recumbent golden setae, lengths of segments I–IV: 0.52, 0.96, 0.70, 0.74.

Pronotum black, width/length (midline) 1.56/0.56; lateral margins almost straight, very slightly sinuate, without light markings; narrow collar present, separated from remainder of anterior lobe by punctate sulcus; anterior lobe tumescent, set off by curving punctate suture from broadly convex posterior lobe; posterior margin of posterior lobe broadly concave; surface of entire pronotum covered with semirecumbent golden setae. Scutellum black, shining, width/length 1.00/0.93; anterior lobe raised, separated from posterior lobe by sinuate sulcus; posterior lobe not raised; surface of both lobes covered with semirecumbent golden setae somewhat longer than on pronotum.

Hemelytra black to blackish brown, faintly shining; clavus length along outside margin 1.70, length of commissure 0.59, each side bearing an elongate yellow spot basally along inner margin and another elongate yellowish spot next to commissure near apex, inner ⅔ of each side dull pruinose, set off from faintly shining outer ⅓ by longitudinal row of punctations; corium uniformly faintly shining; inner corium with 2 roughly ovate spots and sometimes 1 posterior elongate spot evenly spaced along radial vein, plus 1 or 2 distal ovate spots in a more medial parallel row. Outer corium with 1 large white spot at base of embolar fracture, embolium broadly leucine over entire length; wing membrane fumate, darker basally, lateral margin with narrowly triangular thickened pale area extending from base to near apex, veins darker, forming 4 distinct closed cells; surface of clavus, corium and embolium set with moderate length fine recumbent golden setae.

Ventral surface of head and thorax black, abdomen brown and hypocostal ridge

leucine; rostrum brown, length 1.53, attaining hind coxae; entire ventral surface covered with short fine recumbent golden setae. Legs predominantly yellowish white with following portions marked with brown: all coxae basally, all of fore femur except scattered light markings basally and distally, distal ⅓ of middle and hind femora, all tibiae infuscated, and tarsi dorsally on all legs; all leg segments covered with fine semierect golden setae, plus scattered erect black spines on fore, middle and hind tibiae; claws slender, gently curving, brown.

Male genitalia as in Figures 32–35.

Macropterous female. Similar to male except larger and ventral abdominal sterna broadly marked with leucine to yellowish medially, less so laterally. Total length 5.0; width (across hemelytra), 2.6.

Discussion. Rupisalda atra is the first saldid reported from the Comores. It is a typical member of the circumtropical genus *Rupisalda* which has several members on the African mainland. It is also the only species known from the Ethiopian region that lacks yellowish or leucine markings on the lateral margins of the pronotum.

Habitat data. Not known.

Etymology. The name *atra* (L., feminine), black, refers to the coloration of this insect.

Holotype. Macropterous male, COMORES ISL., Anjouan: Riv. Pomoni, oberlauf Anjouan, F/An 24, III-25-1974, F. Starmühlner (USNM). Paratypes. COMORES ISL., Anjouan: 1 female, same data as holotype (NHMW); 1 female, Matasamudu Riv., F/An 4, III-4-1974, F. Starmühlner (JTPC).

Rupisalda slateri, new species

Figs. 21, 36–38; map 3

Description. Of moderate size for genus, shape ovate, length 3.63 mm; maximum width (across hemelytra) 1.70 mm; ground color shining black, sparingly marked with dull white and dark yellow.

Head black, width/length 1.00/0.50, bearing 2 (1 + 1) small dark yellow spots on upper frons at bases of trichobothria, two (1 + 1) additional small ovate yellow spots along inner eye margins on either side of vertex; ocelli of moderate size, dark yellowish; eyes large, protrusive, dark red, width/length 0.28/0.43; frons and vertex covered with numerous fine semi-recumbent golden setae intermixed with a few longer erect golden setae on vertex; antennae slender, brown, covered with short recumbent golden setae, lengths of segments I–IV: 0.33, 0.73, 0.57, 0.53.

Pronotum black, width/length (midline) 1.60/0.40; lateral margins weakly convex, bearing 2 (1 + 1) elongate yellowish spots parallel to and adjoining central portions; small collar present, separated from remainder of anterior lobe by punctate sulcus; anterior lobe weakly tumescent, set off by curving punctate suture from broadly convex posterior lobe; posterior margin of posterior lobe broadly concave; surface of entire pronotum covered with short semi-recumbent golden setae. Scutellum black, shining, width/length 1.03/0.90; anterior lobe only weakly raised, separated from posterior lobe by sinuate sulcus, bearing shallow semicircular depression medially along posterior margin, posterior lobe domed, lateral margins flattened to form thin lip adjoining hemelytra; surface of both lobes covered with short semirecumbent golden setae.

Hemelytra black, shining; clavus length along outside margin 1.63, length of commissure 0.50, each side bearing a small yellow dot at extreme anterolateral angle, a small elongate dark yellow spot basally along inner margin and another roughly ovate yellowish spot next to commissure near apex, inner ⅔ of each side dull pruinose, set off from shining outer ⅓ by longitudinal row of punctations; corium with roughly circular dull pruinose spots centrally and posteriorly, each side bearing 3 elongate yellowish white spots inside of radial vein, these spots arranged longitudinally, relatively evenly spaced and paralleling outer margin of clavus, a single roughly circular bright white spot at base of embolar fracture, three additional small irregular yellowish white spots inside radial vein near tip of clavus; embolar margin with narrow dark yellow longitudinal stripe along basal ¾, this stripe narrowly interrupted by black posteriorly, then expanded into large dark yellow spot, this spot nearly confluent posteriorly with white spot at base of costal fracture; wing membrane fumate, lateral margin with narrowly triangular thickened dark yellow area extending from base to near apex, veins darker, forming 4 distinct closed cells; surface of clavus, corium embolium and thickened membranal area bearing numerous short semierect black setae.

Ventral surface of head, thorax and abdomen black, hypocostal ridge creamy white; rostrum brown, length 1.27, attaining middle coxae; entire ventral surface covered with short fine recumbent golden setae. Legs predominantly black on dorsal surfaces, with narrow annulations of yellowish white at bases and tips of femora and tips of tibiae, ventral surface of hind femora and tibiae mostly pale yellowish white, all tarsi brown; all leg segments covered with fine semierect golden setae, plus scattered erect black spines on fore, middle and hind tibiae; claws slender, gently curving, golden.

Male genitalia as in Figures 36–38.

Discussion. Rupisalda slateri most closely resembles *Rupisalda thika* Polhemus from Kenya, but differs from the latter by the rounded anterolateral angles of the pronotum which are wider than the head including eyes (vs. straight anterolateral angles narrower than head in *thika*), female hypocostal region (hr) feebly produced ventrally and not terminating abruptly (vs. produced into a lamina distally and terminating abruptly), female hr terminating at 0.70 of the distance from the base to the costal fracture (vs. 0.57), embolium dark at extreme basal angle (vs. light), and costal margin light along membrane beyond costal fracture (vs. dark in *thika*); compare figures 3A & B in J. Polhemus 1981 with Figure 21 in this paper.

Habitat data. This species has been found only on vertical rock surfaces, usually around waterfalls, in the wet east coast region of Madagascar. It was not common except at a waterfall 45 km west of Moramonga where it occurred in numbers on the vertical spray wetted rockface. Unfortunately the footing at this collecting site was so treacherous that our collections were limited.

Etymology. This patronym honors the outstanding contributions to entomology, especially hemipterology, by our esteemed colleague and friend, James Alexander Slater.

Holotype. Macropterous male, MADAGASCAR, Tananarive Prov.: waterfall, 45 km west of Moramonga along Tananarive highway below hydro plant, 1,097 m, CL 2252, XI-3-1986, J. T. & D. A. Polhemus (USNM).

Paratypes. MADAGASCAR, Tananarive Prov.: 2 males, 2 females, 1 nymph,

same data as holotype (JTPC, TSIM). Fianarantsoa Prov.: 1 female, Namarona River, 6 km west of Ranamofana, 900 m, CL 2249, X-31-1986, J. T. & D. A. Polhemus (JTPC); 2 females, Tamara Creek at Ambatolahy, 4.5 km west of Ranamofana, 884 m, CL 2251, X-31-1986, J. T. & D. A. Polhemus (JTPC).

Rupisalda vincenti, new species
Figs. 22, 39–41; map 3

Description. Large for genus, shape ovate, length 4.30–4.80 mm; maximum width (across hemelytra) 1.80–2.17 mm; ground color shining black, sparingly marked with white and dark yellow.

Head black, width/length 1.06/0.63, bearing 2 (1+1) small yellow spots on upper frons at bases of trichobothria, 2 (1+1) additional small ovate yellow spots present along inner eye margins on either side of vertex; ocelli large, pale grey; eyes large, protrusive, pale grey, width/length 0.30/0.57; frons and vertex covered with numerous fine semirecumbent golden setae intermixed with long erect black setae; antennae slender, brown, covered with short recumbent golden setae, lengths of segments I–IV: 0.37, 0.83, 0.60, 0.57.

Pronotum black, width/length (midline) 1.80/0.50; lateral margins weakly convex, bearing 2 (1+1) elongate yellowish spots parallel to and adjoining central portions; small collar present along anterior margin, separated from remainder of anterior lobe by punctate sulcus; anterior lobe tumescent, set off by curving punctate suture from broadly convex posterior lobe; posterior margin of posterior lobe broadly concave; surface of entire pronotum covered with semirecumbent golden setae intermixed with longer erect black setae. Scutellum black, shining, width/length 1.27/1.00; anterior lobe raised, separated from posterior lobe by sinuate sulcus, bearing semicircular depression medially along posterior margin; posterior lobe domed; surface of both lobes covered with semi-recumbent golden setae intermixed with longer erect black setae.

Hemelytra black, shining; clavus length along outside margin 1.83, length of commissure 0.50, each side bearing a small yellow dot at extreme anterolateral angle, a small elongate dark yellow spot basally along inner margin and another roughly ovate yellowish spot next to commissure near apex, inner ⅔ of each side dull pruinose, set off from shining outer ⅓ by longitudinal row of punctations; corium dull pruinose centrally and posteriorly, each side bearing 3 roughly ovate yellowish spots inside of radial vein, these spots arranged longitudinally, relatively evenly spaced and paralleling outer margin of clavus, a single roughly circular white spot at base of embolar fracture, other very slender yellow spots of variable size occasionally present just inside of and paralleling radial vein, and near apex of clavus; embolar margin uniformly yellowish white, this pale area occasionally confluent posteriorly with white spot at base of embolar fracture; wing membrane fumate, lateral margin with narrowly triangular thickened pale area extending from base to near apex, veins darker, forming 4 distinct closed cells; surface of clavus, corium and embolium bearing numerous long erect black setae.

Ventral surface of head and thorax black, abdomen and hypocostal ridge creamy white; rostrum brown, length 1.67, attaining hind coxae; entire ventral surface covered with short fine recumbent golden setae. Legs predominantly yellowish white

with following portions marked with brown: fore and hind coxae basally, distal ⅔ of fore femur, distal ⅓ of middle and hind femora, central portion of fore and middle tibiae plus narrow annulations at tips and bases, and entirety of tarsi on all legs; all leg segments covered with fine semierect golden setae, plus scattered erect black spines on fore, middle and hind tibiae; claws slender, gently curving, golden.

Male genitalia as in Figures 39–41.

Discussion. Rupisalda vincenti is apparently most closely related to *Rupisalda machadoi* Drake and *Rupisalda africana* Drake from Africa, the only two other *Rupisalda* species known from the Ethiopian Region with long dorsal setae. *Rupisalda africana* has a stridulatory mechanism consisting of a rastrate patch on the hind femur and serrate costal hemelytral margin, structures lacking in *R. vincenti. Rupisalda machadoi* has very long setae on the legs, especially noticeable on the hind tibia, whereas *R. vinventi* has only short setae on the legs, however the size, shape and coloration of these two species is quite similar.

Habitat data. This species is common and widespread in central, northern and eastern Madagascar, living on the steep rock surfaces of midstream boulders, and around cascades and waterfalls; it may occur also on Nosy-Be (Paulian, 1949).

Etymology. The name honors Dr. Vincent Razafimahatratra who has done much to advance the study of entomology in Madagascar, and who unselfishly gave his time and expertise to further our studies in that country; our research could not have succeeded without him.

Holotype. Macropterous male, MADAGASCAR, Tananarive Prov.: small waterfall and seeping rock face below the Queen's Palace, 1,310 m, CL 2233, X-24-1986, J. T. & D. A. Polhemus (USNM).

Paratypes (all collected by J. T. & D. A. Polhemus). MADAGASCAR, Tananarive Prov.: 47 males, 45 females, 28 nymphs, same data as holotype (JTPC, TSIM). Diego Suarez Prov.: 10 males, 11 females, 3 nymphs, small forest stream, 5 km N of Joffreyville, 488 m, CL 2281, XI-16-1986 (JTPC); 6 males, 6 females, 1 nymph, Mt. d'Ambre Forest Reserve, stream at Petite Cascade, 991 m, CL 2280, XI-15-1986 (JTPC); 4 males, 6 females, 1 nymph, Mt. d'Ambre Forest Reserve, stream at Grand Cascade, 671 m, CL 2278, XI-13-1986 (JTPC). Fianarantsoa Prov.: 1 male, 2 nymphs, roadside waterfall, 10 km S of Ambositra, 1,448 m, CL 2244, X-30-1986 (JTPC); 2 males, 7 km W of Ranomafana, 1,100 m, 1–7 November 1988, W. E. Steiner, from stream with mossy rocks and sandy bottom, montane rainforest (USNM).

KEY TO THE SPECIES OF *SALDULA* OF MADAGASCAR, MASCARENES
(Genus not known from the Comores)

1a. Basal ⅔ or more of clavus dark, without light markings 2
1b. Basal part of clavus not completely dark, with at least a small basal light colored streak or spot .... *madagascariensis* Cobben
2a. Embolium leucine basally, usually completely leucine, but occasionally interrupted at distal ⅔ by a small dark fascia; outer corium predominantly leucine, often with two variably developed brownish regions medially .... *niveolimbata* (Reuter)
2b. Embolium black or brownish basally; usually with a narrow to broad median dark area; outer corium predominantly dark 3
3a. Lateral margins of pronotum distinctly convex; embolium mostly leucine, narrowly black basally, usually with narrow to broad median blackish area; outer corium black,

basally and often distally lighter, with contrasting subdistal ovate white spot .... *ornatula* (Reuter)

3b. Lateral margins of pronotum straight; embolium not predominantly leucine, broadly brownish basally, with a broad brown area at distal ⅔; outer corium brownish, basally lighter, with small median and subdistal irregular light areas, but without subdistal ovate white spot .... *subcarinata* (China)

Saldula madagascariensis Cobben
Figs. 16–18; map 4

Saldula madagascariensis Cobben, 1987. Revue Zool. Afr. 100:417. Type, female, Isalo, Madagascar, in Muséum National d'Histoire Naturelle, Paris.

Additional description. See Cobben (1987a, pp. 417–419, fig. 6) for original description and habitus of light form; only additional details given here. Coloration of dark form: Head with light markings reduced, only elongate preocellar spots (1+1) and small lateral spots (1+1) on frons light, remainder of vertex and frons black. Pronotum with light stripe on humeral margins only weakly indicated, brown. Hemelytra with embolium leucine, interrupted at distal ⅔; inner and outer corium with lightest areas (as shown by Cobben, fig. 6) frosted white, remainder brown, veins black; clavus with basal light spot set in pruinose area, distal elongate spot brown except frosted white on distal extreme. Legs, basal segment of antennae leucine to testaceous, antennae dark on distal 3 segments, segment IV light medially.

Small male: length 2.66, width 1.30. Head width 0.93; length 0.48; minimum interocular space 0.19; eye length 0.48, width 0.37. Length visible rostral segments I–III: 0.11, 1.00, 0.48. Length antennal segments I–IV: 0.30, 0.52, 0.44, 0.54. Pronotum length 0.81; posterior width 1.04, anterior width 0.63, across collar 0.56. Scutellum length (visible) 0.59; width 0.59. Hemelytra: corium length 1.74, clavus length 0.81, length claval commissure 0.37, distance apex claval commissure-apex membrane 0.85. Length of legs: metafemur 0.89, metatibia 1.41. Male genital structures as shown in Figures 16–18.

Discussion. We have seen this species from a number of localities. It lives on horizontal to sloping rock surfaces where there are permanent seeps. On Mt. d'Ambre we found it in the mouth of a shallow cave where ceiling drip and seeps maintained damp rocks interspersed with mosses.

There is considerable variation in coloration so that at first it appeared that two species were present, however all structures were identical in these forms and there are intergrades in coloration in the same population. The lightest form is the one figured by Cobben (1987a: fig. 6), with fasciae near the posterolateral angles of the pronotum, acetabulae anteriorly light and abdominal ventrites yellowish. In the darkest form, all of these structures are black to blackish brown. Cobben described this species from a single damaged female so we have added some details here and figure the male genitalia.

Material examined. MADAGASCAR, Diego Suarez Prov.: 8 males, 8 females, 12 nymphs, Mt. d'Ambre Forest Reserve, stream at Petite Cascade, 991 m, CL 2280, XI-15-1986 (JTPC, TSIM). Fianarantsoa Prov.: 1 female, Namarona River, 6 km W of Ranomafana, 900 m, CL 2249, X-31-1986 (JTPC). Tamatave Prov.: 4 males, 2 females, 2 nymphs, rocky stream 33 km E of Moramanga on Tamatave Hwy., 825

m, CL 2254, XI-3-1986 (JTPC); 1 male, streamlet 52 km W of Brickaville on Tamatave Hwy., 183 m, CL 2258, XI-4-1986 (JTPC); 2 males, 6 females, Ampasimbe River, 80 km E of Moramanga on Tamatave Hwy., 198 m, CL 2263, XI-5-1986 (JTPC).

Saldula niveolimbata (Reuter)
Map 4

Acanthia niveolimbata Reuter, 1900. Bull. Soc. Entomol. Fr. 1900:156. Type, sex unknown, Senegal, repository unknown (Montandon Coll.?).
Saldula niveolimbata Drake & Hoberlandt, 1951. Acta Entomol. Mus. Nat. Pragae 26(376):8.

Discussion. Cobben (1987a, p. 419) listed this species from Madagascar on the basis of material from the Leningrad Museum taken along with *Saldula ornatula* (Reuter) in Tananarive Province. We have seen a single additional specimen from Fianarantsoa Province. This widespread species occurs also on the granitic Seychelles, as well as Africa, Asia, Australia and Samoa.

Material examined: MADAGASCAR, Fianarantsoa Prov.: 1 male, 7 km W of Ranomafana, 1,100 m, 22–31 October 1988, W. E. Steiner, from flight intercept-yellow pan trap in Malaise trap in small clearing, montane rainforest (USNM).

Saldula ornatula (Reuter)
Map 4

Acanthia ornatula Reuter, 1881. Berl. Entomol. Zeitschr. 25:160. Type, sex unknown, Egypt, in Swedish Natural History Museum, Stockholm.
Saldula ornatula Drake & Hoberlandt 1951. Acta Entomol. Mus. Nat. Pragae 26(376):9.

Discussion. This species was present on seeps on an open sunny exposed rock face below the Queen's Palace in Tananarive, but it was not abundant and was difficult to collect. We did not see it on the open exposed shores of ponds or streams elsewhere, although in other regions the preferred habitat seems to be muddy shores. We expect *ornatula* to be found eventually on the Comores and Mauritius, as it is widespread in Africa and Asia, and previously listed from Madagascar by Drake (1960).

Material examined. MADAGASCAR, Tananarive Prov.: 2 males, 4 females, 3 nymphs, small waterfall and seeping rock face below the Queen's Palace, 1,310 m, CL 2233, X-24-1986, J. T. & D. A. Polhemus (JTPC, TSIM). REUNION: 3 males, 7 females, 1 nymph, Cilaos, XI-17-1990, E. Heiss (JTPC).

Saldula subcarinata (China)
Fig. 50

Acanthia (Saldula) subcarinata China, 1924. Ann. Mag. Nat. Hist. (9)14:447. Type, female, Rodriguez, in British Museum (Natural History), London.
Saldula subcarinata Drake & Hoberlandt, 1951. Acta Entomol. Mus. Nat. Pragae 26(376):10.

Discussion. This poorly known species is apparently endemic to the isolated island

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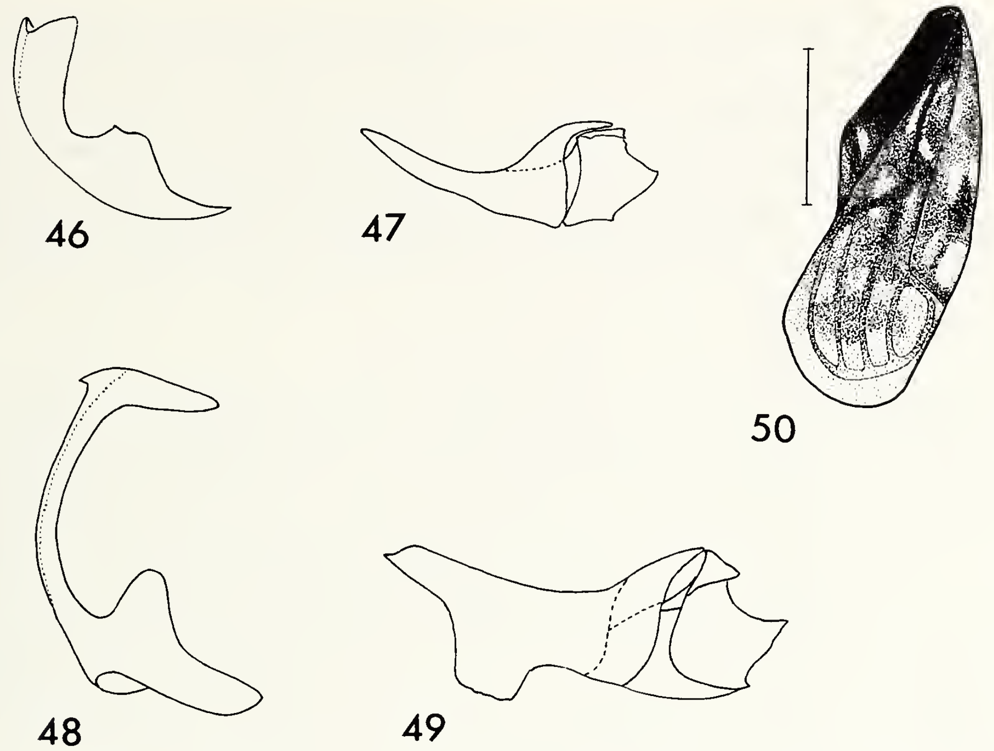

Figs. 46–50. Saldidae. 46–49. Genitalic structures, endosoma. 46–47. *Capitonisaldoida cryptica.* 46. Endosomal sheath. 47. Apicolateral sclerites, side view. 48–49. *Capitonisalda aethiopica* (Carlini), Malawi. 48. Endosomal sheath. 49. Apicolateral sclerites, side view. 50. *Saldula subcarinata,* hemelytra. (Figs. 46–49, courtesy Per Lindskog.)

of Rodriguez. One of us (JTP) has examined the female holotype, which is so far the only known specimen. China's description is adequate, and the species clearly belongs to the genus *Saldula.* It may be separated from its congeners by the distinctive hemelytral pattern (Fig. 50).

Salduncula seychellensis Brown
Fig. 15; map 3

Salduncula seychellensis Brown, 1954. Ann. Mag. Nat. Hist. (12)7:855. Type, female, Mahé, Seychelles, in British Museum (Natural History), London.

Discussion. We have before us a number of specimens from the Seychelles, and a pair from Madagascar. These are in general agreement as stated by Brown (1960). Brown (1954) had only the unique female type from the Seychelles, however he (Brown, 1960) later figured the male paramere of a specimen from Madagascar [a record overlooked by both Polhemus (1981) and Cobben (1987b) in preparing their checklists of African Saldidae]. The junior author has collected several long series on Aldabra Atoll, and a shorter series on Cosmoledo Atoll. With this additional material available from the Seychelles and the atolls of the Aldabra group we have been able to confirm the agreement of the male genitalia and other characteristics

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Figs. 42–45. Saldidae, genitalic structures, endosoma. 42–43. *Capitonisaldoida cryptica.* 42. Side view. 43. Median sclerites, dorsal view. 44–45. *Capitonisalda sp.* 44. Side view. 45. Median sclerites, dorsal view. (Figs. 42–45, courtesy Per Lindskog.)

among these disjunct populations. In males from the Seychelles the filum gonopori is coiled slightly more than 2 times. The parameres of males from both Madagascar and the granitic Seychelles (Fig. 15) are of a slightly different shape but much more hirsute than the paramere figured by Brown (1960: fig. 1C). The endosomal sclerites are typical of the Saldinae. The hemelytral markings of specimens from a single series encompass the variation illustrated by Brown (1960: fig. 1A, B) confirming Brown's assessment that there are not even subspecific differences between the Madagascar and the Seychelles populations.

The nymphs have small widely separated dorsal scent gland openings (1+1) and a well developed larval organ situated slightly more medially than most Saldinae.

Habitat. This genus lives on intertidal rocks, secreting itself in pockets and crevices when disturbed or submerged by rising tide waters (see also Paulian, 1959). On Aldabra Atoll this species was found only on the south and east coasts, which receive heavy wave action from the southeast monsoon and lack an offshore reef crest (D. Polhemus, 1990). A diligent search of suitable intertidal rocks in the Mascarenes and Comores should reveal the presence of this species there also. In the Malay Archipelago (Singapore, Sabah) this species is replaced by other undescribed species that live in similar situations (J. Polhemus, 1991).

Material examined. MADAGASCAR, Majunga Prov.: 1 male, 1 female, Nosy-Be, Pointe á la Fievre, récife corallien, R. Paulian (JTPC). SEYCHELLES, Mahé: 1 male, 3 females, Bean Valley Bay, on rock, HWM, VIII-20-1985, L. Cheng (JTPC). St. Anne Is.: 4 males, 10 females, 27 nymphs, among small barnacles on boulders, HWM, VIII-19-1985, L. Cheng (JTPC). ALDABRA ATOLL, Grande Terre Is.: 9 males, 7 females, 45 immatures, rocky coast at Cinq Cases, low tide, 1500 hr, 13 March 1989, CL 8030, D. A. Polhemus (USNM, JTPC); 21 males, 10 females, 22 immatures, rocky coast at Dune Jean Louis, 9°27′16″S, 46°23′70″E, low tide, 1230–1430 hr, 24 March 1989, CL 8040, D. A. Polhemus (USNM, JTPC). COSMOLEDO ATOLL, Menai Is.: 1 female, 8 immatures, rocky coast at Johannes Point settlement site, 9°41′68″S, 47°32′26″E, low tide, 1100 hr, 27 March 1989, CL 8041, D. A. Polhemus (USNM).

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western Indian Ocean. Holotypes are deposited in the USNM unless otherwise noted; paratypes are in the collection of the Parc de Tsimbazaza, Tananarive (TSIM), and the J. T. Polhemus collection, Englewood, Colorado (JTPC). Paratypes and other specimens will also be distributed to the American Museum of Natural History, USNM and the Pericart Collection as material permits. This research was supported in part by a grant for field work from the National Geographic Society, Washington, D.C. (NGS # 3398-86), and by a grant from the National Science Foundation (BSR-9020442) to whom we are deeply grateful.

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NOTOSPHINDUS SLATERI, A NEW GENUS AND SPECIES OF SPHINDIDAE (COLEOPTERA: CUCUJOIDEA) FROM AUSTRALIA

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Abstract.—*Notosphindus,* a new genus of Sphindidae (Coleoptera: Cucujoidea) from Australia, is described based on a single new species, *N. slateri.* A diagnosis for *Notosphindus* is provided using those characters believed to be of phylogenetic importance at the generic level. Dorsal and ventral habitus illustrations and morphological illustrations are provided. Several character transformations in the family Sphindidae are discussed.

The coleopteran family Sphindidae with 52 described species is relatively small, but is represented in every major biogeographic region (see McHugh, 1991). Species of the genus *Aspidiphorus* have been reported from numerous old world localities including Tasmania (Champion, 1924; Scott, 1926) and Queensland (Scott, 1926). These records were apparently based on undescribed material, some of which may have been at The Natural History Museum (London). Curiously, these seem to be the only Australian records for the family to date. Subsequent faunal works for the region, including Britton (1979), do not include any species of Sphindidae in summaries of Australian Coleoptera.

In an hypothesis of the phylogenetic relationships of the genera of Sphindidae, McHugh (1991) included an undescribed Australian genus. That analysis found that *Notosphindus,* described as new below, clearly belongs to the subfamily Sphindinae (*sensu* McHugh, 1991) that includes those genera with the following character states: mandibles flattened, galeae apically narrowed, and wings lacking an anal cell and lacking a branched first anal vein. *Notosphindus* may be the sister group of the clade *Carinisphindus* + *Sphindus* or of the clade ((*Carinisphindus* + *Sphindus*) + (*Aspidiphorus* + *Eurysphindus* + *Genisphindus*)). *Notosphindus* possesses several character states intermediate between previously described forms, suggesting alternative interpretations of character transformation series in the Sphindidae.

Measurements given in the text are ranges with the arithmetic mean in parentheses. The units of measure are millimeters. Insect collections are represented by acronyms in the text as follows: (ANIC) Australian National Insect Collection, Canberra; (BMNH) The Natural History Museum, London; (CNC) Canadian National Collection, Ottawa; (CUIC) Cornell University Insect Collection, Ithaca; (FMNH) Field Museum of Natural History, Chicago; (MCZ) Museum of Comparative Zoology, Harvard University, Cambridge; (USNM) Smithsonian Institution, Washington, D.C.

Notosphindus, new genus

TYPE SPECIES: *Notosphindus slateri* McHugh & Wheeler, designated here and described below.

DIAGNOSIS: *Notosphindus* bears a strong resemblance to *Sphindus* and *Carinisphindus.* It may be distinguished from both genera by three characters: (1) the pronotum of *Notosphindus* is abruptly depressed posteriorly and posterolaterally; (2) the mandible is tridentate in *Notosphindus* while in the other two genera only one well-developed tooth occurs; and (3) the pygidium is punctate over most of the dorsal surface as opposed to being impunctate in two large lateral patches that are raised and densely setose in *Carinisphindus* and *Sphindus.* In addition, *Notosphindus* differs from *Carinisphindus* in that the pronotum and scutellum of the former lack a median, dorsal, longitudinal carina; the lateral edge of the pronotum is crenulate in the former but smooth in the latter; the apex of the clypeus in the former is arcuate with a pair of weak lateral notches as opposed to being deeply emarginate and lacking lateral notches; and the antennal club of the former is three-segmented as opposed to two-segmented. *Notosphindus* differs from *Sphindus* in that the male metafemur has a posterior tooth, and the wing venation includes the first and fourth anal veins. The color pattern in the only known *Notosphindus* species is much more distinct than that in any known *Sphindus* species, but it is impossible to know whether this will serve as a good generic character.

If *Aspidiphorus* truly is represented in Australia it can be easily distinguished from *Notosphindus.* In *Aspidiphorus* the body form is oval and convex; the procoxal cavities are widely opened externally; the pronotal lateral edge is smooth; antennomere VIII is at least as long as wide; the hypomera are concave anteriorly; the pygidium has a median longitudinal groove. For *N. slateri* the body form is elongate, subparallel and more flattened; procoxal cavities are closed externally; pronotal lateral edge is crenulate; antennomere VIII is transverse; hypomera are not concave; and the pygidium lacks a median longitudinal groove.

ETYMOLOGY: From the Greek "notos" (south), and the existing genus name *Sphindus,* a name suggested by J. F. Lawrence in reference to the distribution of the only known species.

Notosphindus slateri, new species
Figs. 1–15

TYPE MATERIAL. Holotype: [AUSTRALIA: Mt. Field, N.P.] male (ANIC) with following label data: "42.41S 146.40E Mt.Field N.P. Lake Dobson Rd. 710m TAS 31 Jan. 1980 Lawrence & Weir" "J.F. Lawrence Lot 80- 15 Lycogala sp." Paratypes: 34 males, 19 females (ANIC); 2 males, 2 females (BMNH); 2 males, 2 females, (CNC); 2 males, 2 females (CUIC); 2 males, 2 females (FMNH); 2 males, 2 females (MCZ); and 2 males, 2 females (USNM) all with same label data as holotype.

DESCRIPTION: Body narrowly oval, convex, head visible from above (Fig. 1). Length = 1.5–2.3 (1.88). Head, pronotum, scutellum and anterior half of elytron light reddish brown; elytron with dark gray to blackish transverse band extending in length from lateral edge to almost the medial edge and ranging in width from broad at the lateral edge (extending from the midpoint of the elytron to a point about two-thirds its length) to much narrower near the medial edge (Fig. 1); apical end of elytron reddish-brown; eyes black; venter, legs, antennal stem, and mouthparts light reddish brown; body shiny. Dorsal setation of very short, pale, sparse setae.

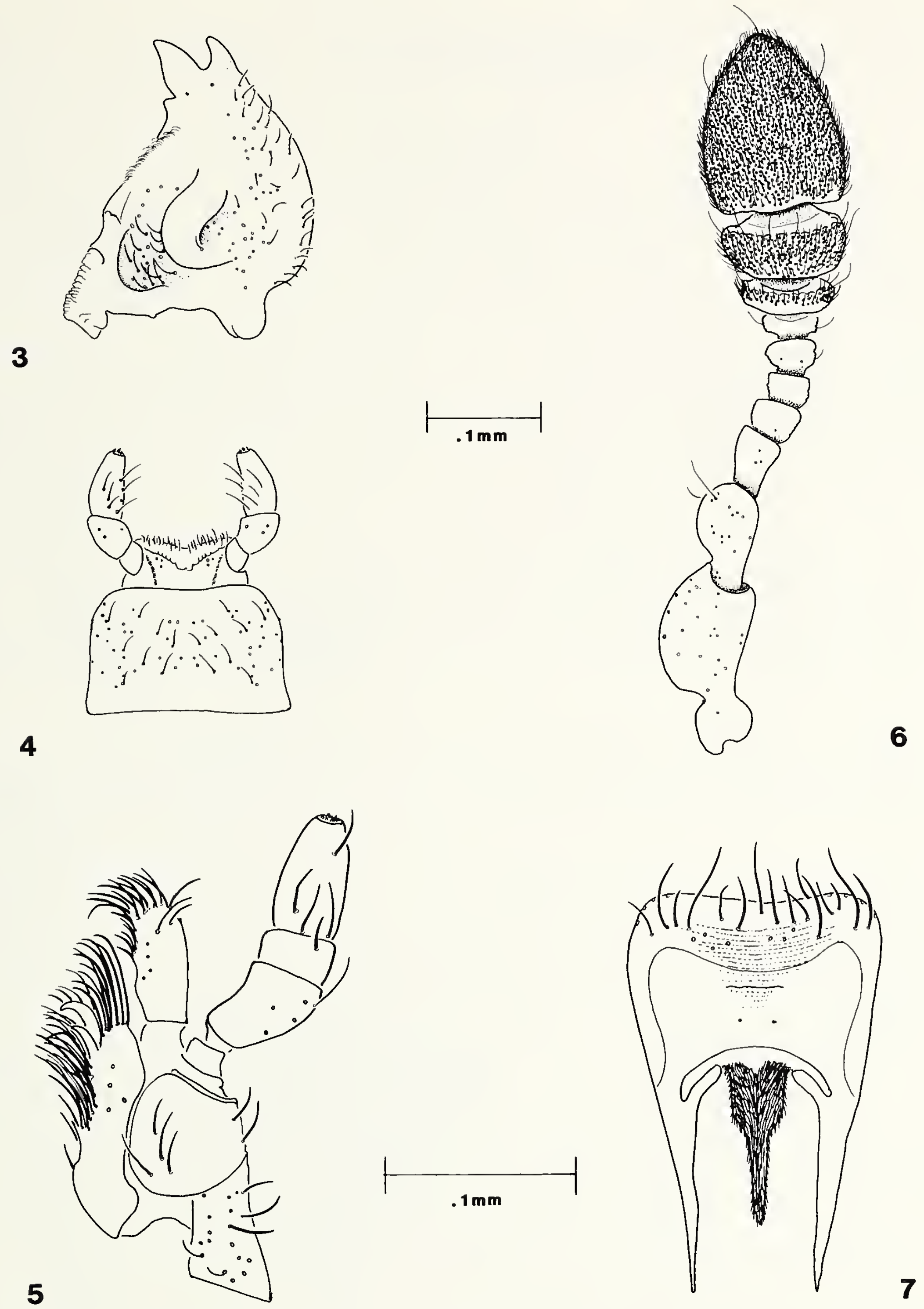
Fig. 1. *Notosphindus slateri.* Dorsal habitus of adult male.

Head with a pair of strong dorsal antennal grooves extending from between antennal insertion and clypeus to beyond top of eyes and several other shorter, less distinct grooves (Fig. 1); medial region lacking grooves, but with sparse shallow punctures; weakly constricted postocularly; ventrally with 2 pairs of antennal pits, posterior pair poorly defined; frontoclypeal suture arcuate; gular sutures appearing externally as pair of short basal depressions; clypeus emarginate laterally, apically arcuate with pair of weak lateral notches; eye coarsely facetted.

Antenna 10-segmented, with robust and asymmetrical antennomeres I–II inflated

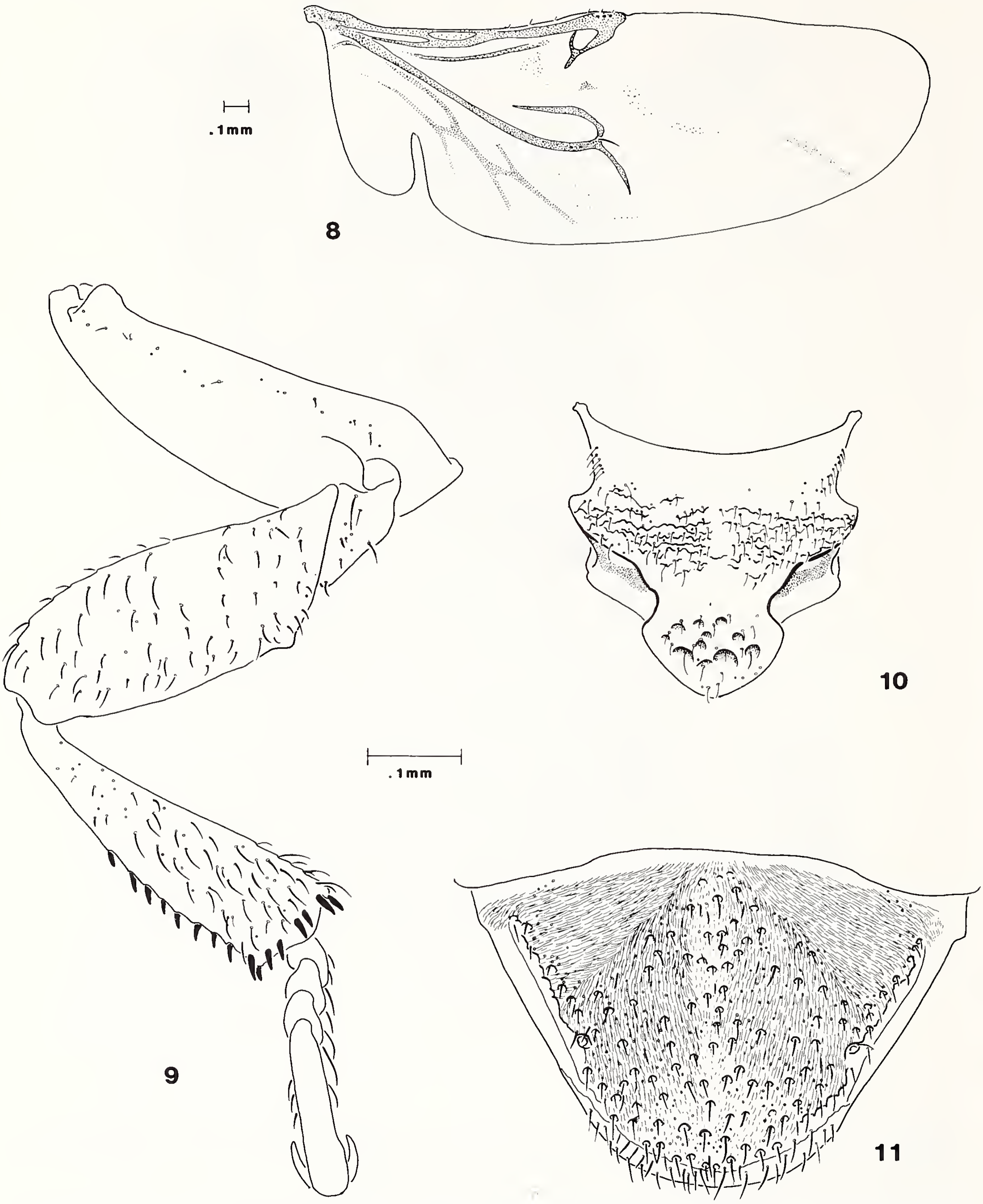
Fig. 2. *Notosphindus slateri.* Ventral habitus of adult male.

on anterior side, antennomere III about 2 times as long as wide, IV–VI submoniliform, VII wider and more transverse than IV–VI, VIII–X large, forming densely pubescent abrupt compact club; VIII wedge-shaped, IX–X symmetrical, X about 3 times length of IX, IX about 2 times length of VIII (Fig. 6). Labrum small, nearly completely concealed by clypeus; weakly bilobed at apex (Fig. 7). Mandible robust, tridentate; tooth II largest; tooth I somewhat deflexed; teeth flattened and all visible from dorsal view; tubercle with abrupt depression forming lateral margin (Fig. 3), prosthecal fringe of short curled setae. Maxilla with slender galea and lacinia, both densely setose at apex; lacinia with two stout spines; palpus four-segmented, basal segment smallest, apical segment longest and with sparse apical sensilla (Fig. 5). Labium with transverse mentum; bilobed ligula; apical segment of palpus largest; distal end with sparse sensilla (Fig. 4).



Figs. 3–7. *Notosphindus slateri*. 3. Right mandible, dorsal. 4. Labium, ventral. 5. Right maxilla, dorsal. 6. Right antenna, dorsal. 7. Labrum, ventral.

Pronotum length = 0.4–0.6 (0.5), width = 0.6–0.8 (0.76); slightly narrowed in front, rounded at sides, convex, flattened laterally with acute, weakly crenulate edge, anterior edge weakly emarginate medially (Fig. 1), basal margin arcuate, basal and lateral edges slightly upturned; dorsal surface with weak trace of pronotal lateral depressions, shallow punctures and very fine microsculpturing, abruptly depressed posteriorly and posterolaterally; procoxal cavity nearly closed exteriorly by posterior extension of hypomeron; prosternal process raised but deflexed at apex, punctate, slightly wider at apex than at midpoint (Fig. 2). Mesosternum short, punctate, weakly



Figs. 8–11. *Notosphindus slateri.* 8. Right wing, dorsal. 9. Right male metathoracic leg, anterior. 10. Scutellum, dorsal. 11. pygidium, dorsal.

deflexed near midpoint; mesosternal process flat, broad, weakly emarginate at apex; trochantin exposed. Metasternum inflated, densely punctate anteriorly and laterally, impunctate posteromedially.

Leg long. Coxa transverse. Femur moderately setose, male metafemur with posterior tooth near trochanter (Fig. 9). Tibia dilated apically and with weak groove to

receive tarsus, narrowed basally, moderately setose, with apical crown of stout spurs and several preapical spurs along anterior edge. Tarsi 5-5-5 female, 5-5-4 male. Tarsomeres simple, with apical segment about as long as others combined, tarsomeres with tuft of setae ventrally, claws simple.

Scutellum small, transverse, oval-chordate, with large weak median transverse depression formed by several irregular punctures which lack well-developed posterior margins (Fig. 10). Wing covered with minute setae, with posterior and posterolateral margins fringed with setae, with well-developed jugal lobe, media, cubitus, medio-cubital crossvein, costa, radius, three anal veins, and one anal cross vein (Fig. 8). Elytron length = 1.0–1.6 (1.25), width = 0.8–1.1 (0.95); elongate, covering abdomen, weakly rounded at side, tapered posteriorly, disk convex, with strong subhumeral depression and well-developed humeral callus, epipleuron narrow; dorsal surface with one scutellary and 10 long punctate strial interneurs; strial interspaces flat, with sparse irregular short setation.

Abdomen with 5 visible sternites; sternite I about 2–3 times length of other sternites, with large punctures; II–V with a basal row of depressions (Fig. 2), impunctate distally; sternites not in same plane giving shingled appearance. Pygidium covered with dense short setae and sparse longer setae emerging from punctures, fine setae sparser and setose punctures denser in median longitudinal band and distally (Fig. 11).

Male. Aedeagus turned on left side when retracted into abdomen. Parameres fused and nonarticulated, fused apex slightly swollen, but relatively narrow, positioned in apically concave median lobe (Fig. 12).

Female. Genitalia with a singly lobed coxite, broadly rounded at apex, sparsely covered with short setae (Fig. 15), stylus short preapical, with one long and one short seta (Fig. 14). Spermatheca with spermathecal gland at apex (Fig. 13).

ETYMOLOGY: A patronym for Professor James A. Slater whose diverse interests, scientific contributions, and scholarship have been a source of inspiration to the authors.

DISTRIBUTION: Known from southeast Australia in Victoria, and in Tasmania.

NATURAL HISTORY: As is the case for all species of Sphindidae, *N. slateri* is apparently myxomycophagous. Although records of sphindid species feeding on many different slime molds exist, representing a rather diverse group of host species (see McHugh, 1991), this is only the second species reported in association with a *Lycogala* species. *Sphindus dubius* has been repeatedly collected from *Lycogala* "species" (Jacquelin Du Val, 1863; Crowson, 1967); *Lycogala epidendrum* (Lawrence & Newton, 1980; Benick, 1952); and "*Lycogala miniata*" (LaCordaire, 1857; Kiesenwetter & Seidlitz, 1898; Schaufuss, 1916) which has since been synonymized with *L. epidendrum* (see Martin and Alexopoulos, 1969).

OTHER MATERIAL EXAMINED (all at ANIC): [Tasmania] 3 males, 2 females with data: "AUSTRALIA: Tasm.: Mt. Field NP Lake Dobson Rd. 240m 30.i-5.ii.1980 wet sclerophyll A. Newton, M. Thayer"; 1 male, 1 female with data: "Australia, Tas. Mt. Field N.P. Jan. 8–14, 1984 L. Massner, MT"; 1 male with data: "AUSTRALIA: Tasm.: Lyell Hwy. at Franklin R. 55kmESE Queenstown 400m 19–20.ii.1980 A.Newton, M.Thayer Nothofagus cunninghamii, etc. forest"; 1 female with data: "41.47 S 145.35 E 4km E Rosebery TAS 16 Jan– 1 Feb 1983 I.D.Naumann J.C.Cardale coll."; 1 female with data: "Tasmania Balckburn S. A. Museum specimens"; and 1

male with data: "Australia, Tas. 10km S.Hellyer Riv. Jan.10, 1984 L.Masner, s.s. Old Nothofagus forest with Asplenium". [Victoria] 1 female with data: "AUSTRALIA: Vict.: Coranderrk Res., SE Healesville c240m 13.i.1980 Euc.-tree fern A.Newton, M.Thayer berlesed from leaf litter"; 2 males and 2 females with data: "37.43S 145.42E Cement Ck. 5km N of Warburton V 17 Jan. 1978 Lawrence & Weir J.F.Lawrence Lot 78-16 Lycogala sp."; and 1 male and 1 female with data: "AUSTRALIA VIC Cement Creek 5 km N of Warburton 17 Jan. 1978 Lawrence, Weir".

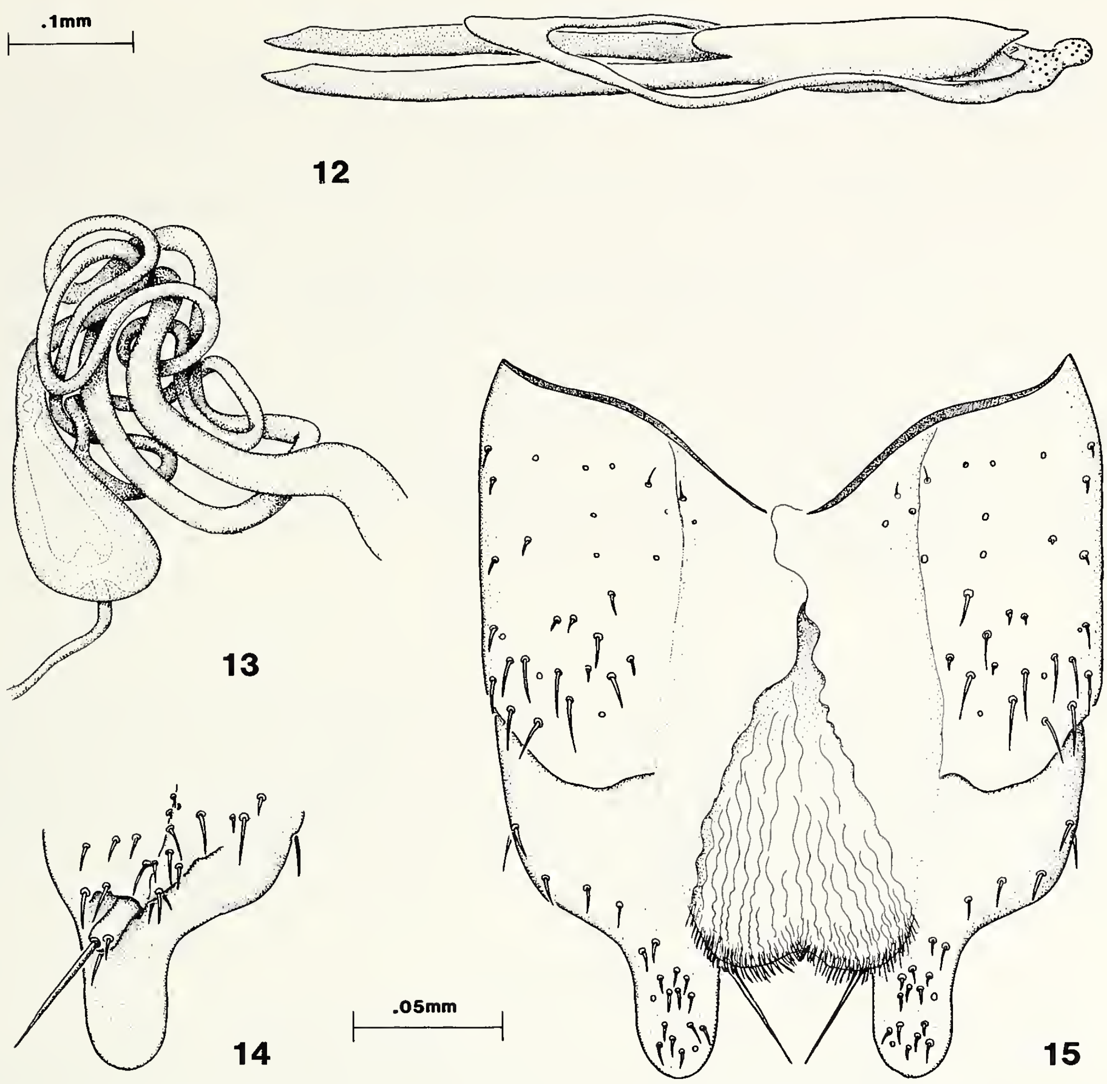
Many specimens in the type series appear to be teneral. They are slightly smaller, lack the typical coloration described above including the elytral markings and are uniformly yellowish-brown. Most of the specimens from the Australian mainland have more transparent elytra on which the dark markings seem to extend posteriorly to the elytral apex. The coloration pattern typical of the Tasmanian specimens and described above is also found in the mainland material as well as intermediate forms. Thus, we regard all these specimens as conspecific.

CHARACTER DISCUSSION

In light of McHugh's (1991) phylogentic hypothesis, using *Ericmodes sylvaticus* (Protocucujidae) as the outgroup, *Notosphindus* is near the junction of the clades *Aspidiphorus* + *Eurysphindus* + *Genisphindus* and *Sphindus* + *Carinisphindus.* Because *Notosphindus* appears to be intermediate between previously known plesiomorphic and apomorphic extremes of several morphoclines within the family, it is of special phylogenetic interest. Thus, it may be useful to discuss the homology and polarity of these features.

The plesiomorphic condition for the mandible in Sphindidae involves a broad apex issuing three stout teeth in an overlapping arrangement as is seen in *Protosphindus* and *Odontosphindus.* The ventral tooth is completely hidden from dorsal view by the large middle tooth. In *Eurysphindus, Genisphindus, Aspidiphorus, Sphindus,* and *Carinisphindus* the apex of the mandible is flattened with all existing teeth visible dorsally (although a tooth is lost in some). In *Notosphindus* and *Sphindiphorus* all the teeth are visible from above but the first tooth is strongly deflexed. This suggests to us that the apical tooth on the flattened mandible of *Aspidiphorus, Eurysphindus,* and *Genisphindus* is homologous with the ventral tooth of *Ericmodes* (the outgroup), *Protosphindus* and *Odontosphindus.* In *Sphindus* and *Carinisphindus* only two teeth are present of which one is well developed, and it is unclear whether the apical-most tooth is homologous with the ventral or the middle tooth of the plesiomorphic condition. However, in *Notosphindus* the "ventral" tooth is smaller in size relative to the other two teeth, suggesting that perhaps this tooth is lost in the *Carinisphindus* + *Sphindus* clade.

Sphindidae seem to have gone through a series of reductions in wing venation. In the plesiomorphic condition (seen in *Protosphindus* and *Odontosphindus*), the wing venation includes the following features: three anal veins (1A apically branched), and two anal cross veins enclosing an anal cell. This plesiomorphic condition of the wing is illustrated by Burakowski and Ślipiński (1987: fig. 6) for *Protosphindus chilensis* and also illustrated by Crowson (1967: fig. 112) for *Sphindus grandis,* a species which appears to actually belong to *Odontosphindus* as suggested by Sen Gupta and Crowson (1977) (see McHugh, 1991). In *Aspidiphorus, Sphindus, Genisphindus,* and



Figs. 12–15. *Notosphindus slateri*. 12. Male genitalia, lateral. 13. Spermatheca. 14. Left coxite and stylus of female genitalia, ventral. 15. Female genitalia, dorsal.

Eurysphindus only one well developed anal vein remains that, judging from its position and form, is homologous with 2A in the outgroup. In *Notosphindus* (Fig. 8) and *Carinisphindus* (see McHugh, 1990: fig. 17) the venation is more complete (plesiomorphic), however, one branch of the first anal vein is absent.

The pygidium is another source of characters of phylogenetic importance for the family. In the plesiomorphic condition, the pygidium is impunctate and dorsobasally covered with short dense setae, and dorsomedially and distally covered with longer and sparser setae. *Notosphindus* has punctures at the base of the longer setae. These punctures are most dense in a median longitudinal strip which also lacks the short dense setae (Fig. 11). In the areas just lateral to this median longitudinal strip the punctation is somewhat reduced. This condition may be an intermediate one between the grooved pygidium seen in *Sphindiphorus* (see Sen Gupta and Crowson, 1977: fig. 15) and the pygidium of *Carinisphindus* and *Sphindus* on which a weakly depressed and punctate median longitudinal strip occurs (see McHugh, 1990: figs. 19, 25). Just lateral to this strip in *Sphindus* and *Carinisphindus* is a large impunctate patch on each side. These patches are covered with the dense short type of setae which are now confined to these patches alone and to a narrow basal area.

CONCLUSIONS

Character states discovered in *Notosphindus* suggest new interpretations of several characters. Tests of these homology statements and polarity hypotheses, however, depend upon the analysis of additional characters. Unfortunately, the paucity of specimens of some sphindid groups prohibits disarticulation and examination of the male and female genitalia, the spermatheca, and the metendosternite. Although the sclerotized parts of the male genitalia are reduced, making it difficult to find useful phylogenetic characters, the female genitalia, spermatheca, and the metendosternite promise to be informative. The addition of information about other semaphoronts has been growing (e.g., Burakowski and Ślipiński, 1987), and it may soon be possible to include in an analysis data from larvae, pupae, eggs, etc. At the moment, however, only the adult stage is described for any species of *Sphindiphorus, Notosphindus, Carinisphindus, Genisphindus,* and *Eurysphindus.*

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REVIEW OF THE GENUS *MICROSCHATIA* (SOLIER) (TENEBRIONIDAE: COLEOPTERA)

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Abstract.—Taxonomic relationships are detailed for 12 species in the genus *Microschatia,* which is distributed from north central Mexico and Baja California to southern Texas, New Mexico, Arizona and California, in arid or subarid habitats. *Pycnonotida* Casey and *Acroschatia* Wilke are treated as junior synonyms of *Microschatia,* and a key to species is provided. Newly described are *M. solieri* Brown and Doyen, *M. cedrosensis* Brown and Doyen, *M. costulata* Brown and Doyen and *M. planata* Doyen and Brown. The first and late instars of *M. championi* are characterized.

Microschatia constitutes a small genus of poorly studied beetles of the tribe Asidini. The genus was proposed by Solier (1836) for his species *punctata.* Horn (1893) briefly described the seven species then known and provided a key. It is worth remarking that *Microschatia* is sufficiently distinct that its species were never included in the catchall genus *Asida,* which contained most American Asidini before being split by Casey (1912) into numerous new genera. Most of Casey's asidine genera appear to be valid and are presently recognized in catalogs. However, his genus *Pycnonotida,* proposed to contain *M. inaequalis* LeConte, is here placed in synonymy under *Microschatia* for reasons discussed below. Likewise, *Acroschatia,* proposed by Wilke (1922) for *M. robusta,* is here considered unjustified and placed in synonymy.

We have examined types of all described species except *M. punctata* Solier, of which the identity is clear from Solier's description and illustration. The intent of the present account is to describe four additional species, redefine *Microschatia,* and to provide an estimate of its cladistic structure and a key to the species.

MATERIALS AND METHODS

Specimens were measured with dial calipers (M.P.J. Gauge and Tool Co., Ltd., England) or with an ocular micrometer. Female internal structures were prepared as described by Tschinkel and Doyen (1980), but stored in glycerine on depression slides. Cladistic analyses were performed using Hennig 86 (J. S. Farris, S.U.N.Y.). Larval rearing was accomplished using containers and procedures described by Brown (1973) and Doyen (1973).

BIOLOGY

With three exceptions, *Microschatia* have remained rare beetles in collections. The exceptional species are *M. championi,* which is locally abundant about palm oases

in Baja California Norte, *M. planata,* which seasonally is extremely abundant on sand dunes in the Vizcaino region of Baja California, and *M. inaequalis* which was formerly common in much of coastal California south of the Los Angeles Basin. The first species is now represented by about 85 specimens, nearly all collected from the area around Arroyo Catavina. *Microschatia planata,* which was first collected in 1973, now numbers more than 200 museum specimens, nearly all from the vicinity of Guerrero Negro. Most recently collected specimens of *M. inaequalis* are from interior locations near Riverside, Riverside County. However, as recently as 30 years ago significant series were collected in coastal localities in Orange and San Diego Counties. Apparently many of these coastal populations have been eliminated by suburban expansion.

In large part because of their rarity in collections, most species of *Microschatia* have very poorly known life histories. Collection dates indicate that the species inhabiting the central plateau of Mexico are active during the high rainfall months of June to September. In contrast, the Pacific coastal species are active primarily during the period from January to June, corresponding to the precipitation pattern of that region. This shift in time of activity occurs in several other Pacific coastal Tenebrionidae, including *Stenomorpha, Trichiasida* (Asidini) and some *Eusattus* (Coniontini).

Most Asidini are relatively short lived as adults, often surviving only a few weeks. No records exist for any of the mainland Mexican species, but *M. inaequalis* and *championi* survive several months in the laboratory, and some individuals of *M. planata* have survived for over six months (J.T.D., unpublished).

Several of the species of *Microschatia* inhabiting the central plateau of Mexico thickly encrust parts of the body with fine particles of soil, whereas those of the Pacific coast have clean cuticle. The function of encrusting, which probably begins in the teneral adult in the pupal chamber, is probably camouflage, since the encrusted surfaces are rendered similar in color to the substrate (see also Lawrence and Hlavac, 1979). The patterns formed by the encrusting material are somewhat taxon specific. For example, in *M. punctata, solieri* and *robusta* portions of the dorsum and femora are covered, whereas in *M. morata, rockefelleri* and *sulcipennis* only the dorsum of some individuals has a light coating of soil. Details of the encrustation patterns appear in the descriptions of pertinent species.

Unlike the taxa discussed by Lawrence and Hlavac the cuticular surface of *Microschatia* species is not organized as a complex system of pores and canals for distribution of adhesive secretions. Rather, the encrusted material is localized in cuticular depressions (either punctures or rugosity), but the source of the adhesive and means of its distribution are not apparent.

Encrusting is frequently accompanied by presence of scale-like setae in Coleoptera (e.g., Zopheridae; Colydiidae; Derodontidae) (Lawrence and Hlavac, 1979), and all encrusting species of *Microschatia* have flattened setae, though not always corresponding to the areas of encrustation. In several species the scaliform setae form striking, unique patterns, which do not obviously contribute to camouflage.

The mainland Mexican species of *Microschatia* mostly occupy semiarid woodland habitats, judging from collection records, but no details of habitat preference or requirements are available. Among the Pacific coastal species, *M. inaequalis* has been collected in many different situations, including maritime bluffs, and on both stoney

and fine grained substrates in the interior of southern California. Plant formations occupied include coastal and interior chaparral, savannah woodland and desert. In contrast, *M. championi* and *M. planata* appear to be much more restricted. The former has been collected almost exclusively around areas with permanent subsurface water, especially palm oases. The latter is narrowly restricted to aeolean sand dunes in the Vizcaino region of Baja California.

Larvae have been positively associated only with *M. championi.* They hatched from eggs deposited by captive females and survived in the laboratory to moderate size, but then failed to continue growing, all eventually dying before pupation. Nothing is known of larval biology under natural conditions.

CLADISTIC RELATIONSHIPS

Estimates of cladistic relationships were based on analysis of the 32 characters listed in Appendix 1. Since *Microschatia* is morphologically isolated in the Asidini, making it very difficult to convincingly designate a sister genus, characters were polarized according to their general distribution in Asidini, delimiting a hypothetical outgroup [defined by primitive states for all characters]. For nearly all the characters it seems clear which state is primitive for Asidini, but it is also apparent that convergence or parallelism has been commonplace in these beetles. For example, while a basally constricted pronotum may be reasonably construed as primitive in Asidini, parallel sided bodies occur in *Asidopsis, Parasida* and *Litasida,* as well as *Microschatia.* Within *Microschatia,* therefore, it is possible that the parallel sided condition is primitive and the waisted condition a secondary reversal, or that parallel sidedness has evolved more than once. An overall assessment of generic relationships within Asidini is in progress (KWB), and may eventually require modifying some of the character polarizations applied here by allowing identification of a real sister taxon to *Microschatia.*

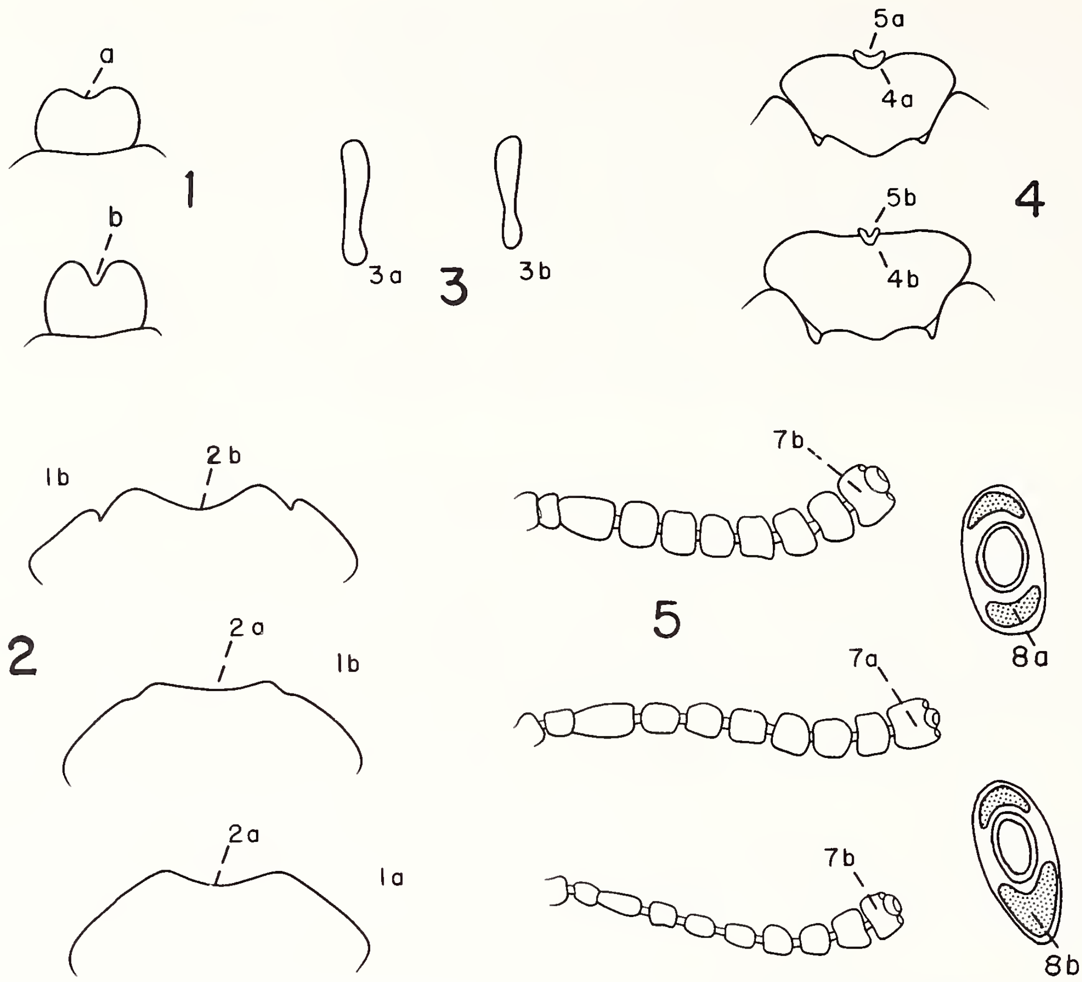
Characters and States

0. *Labrum shape* (Fig. 1). In most Tenebrionidae the anterior margin of the labrum is arcuately convex or truncate. In Asidini it is commonly concave, but not so deeply and narrowly as in *Microschatia.* In many genera dense brushes of anteromedially directed labral setae give the impression of a deep, narrow emargination.

1–2. *Epistomal shape* (Fig. 2). A medially truncate or arcuate anterior margin with the lateral epistomal sutures often obsolete and faintly indicated by indentations is general in Tenebrionidae and apparently primitive in Asidini. The lateral sutures are marked by strong indentations in *Ucalegon,* some *Stenomorpha, Platasida* and *Bothrasida,* as well as *Microschatia.* The epistoma is deeply concave in *Tisamenes* and moderately so in several other genera.

3. *Eye shape* (Fig. 3). Eyes of Tenebrionidae are characteristically deeply emarginated by the epistomal canthus. In *Microschatia* the eyes are very elongate and the degree of constriction is reduced. This appears to be the primitive condition in Asidini, and in most other genera the eyes are elongate or short oval, without trace of constriction.

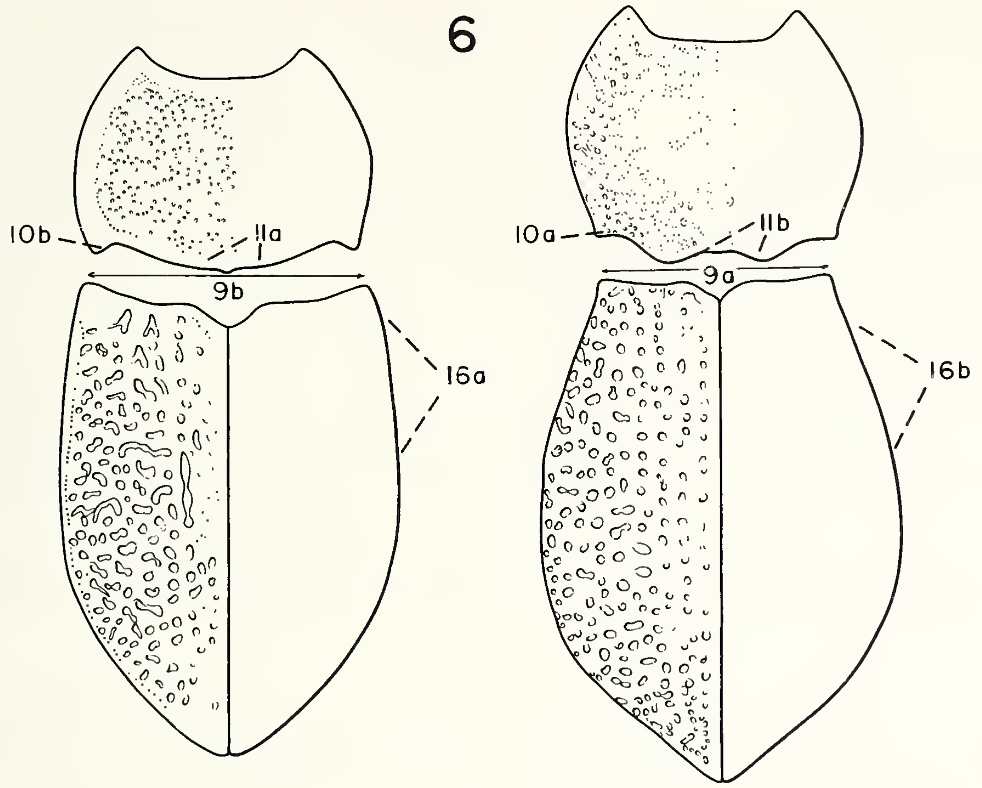
4–5. *Mentum and ligula* (Fig. 4). The small size of the ligula and its high degree of sclerotization appear to be apomorphies for Asidini. The ligula is also sclerotized

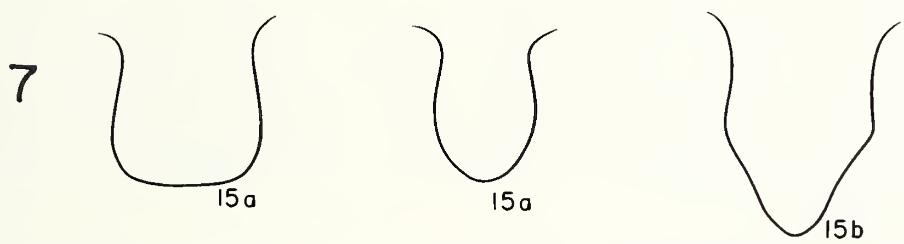


Figs. 1–5. Taxonomic characters of *Microschatia*. 1. Labra of *inaequalis* (a), *rockefelleri* (b). 2. Epistomal margins of *solieri* (top), *rockefelleri* (middle) and *inaequalis* (bottom). 3. Eye shape of *championi* (left) and *solieri* (right). 4. Labia of *rockefelleri* (top) and *solieri* (bottom). 5. Antennae of *solieri* (top), *rockefelleri* (middle) and *inaequalis* (bottom). Small numbers and letters indicate characters and character states as listed in Appendix 1.

(less strongly so) in Coniontini, but is much larger relative to the mentum. In most Tenebrionidae the mentum is broadly emarginate, with the ligula exposed in the emargination. In most Asidini there is a narrow notch in the middle of the emargination. The notch becomes especially deep in some *Microschatia,* and the ligula is retracted beneath the mentum and barely visible. The ligula is also largely concealed in the asidine genera *Stenosides* and *Astrotus.*

6–8. *Antennal configuration* (Fig. 5). Antennae are typically short in Asidini, as they are in *Stenosides* and *Astrotus,* which are similar to *Microschatia* in a few other features. Therefore we consider the longer antennae in some *Microschatia* to be derived. The antennae of *Microschatia* are also somewhat longer in males than in females. Antennal segment 10 in Tenebrionidae (including Asidini) is usually longer than wide or subquadrate. Thus, the relatively broad segments of *Microschatia* are considered derived. However, this feature is subject to much homoplasy throughout the family. The tomentose sensory patches on segment 10 are usually subequal in size, which we consider plesiomorphic. In some *Microschatia* the outer patch is enlarged as in *Gonasida, Philolithus, Trichiasida,* and *Tisamenes.* In *Gonasida, Philolithus* and *Trichiasida* the inner patch is split into two smaller ones. In *Sicharbas,*





Figs. 6, 7. Taxonomic characters of *Microschatia.* 6. Dorsa of *rockefelleri* (left) and *championi* (right). 7. Prosternal processes of *solieri* (left), *inaequalis* (middle) and *planata* (right). Conventions as in Figures 1–5.

Platasida and *Heterasida* the tomentose patches are consolidated into a ring. Generally the disposition of these tomentose patches appears to be a useful character for Asidini.

9–12. *Pronotal configuration* (Fig. 6). As discussed above, basally constricted pronota are regarded as plesiomorphic in Asidini, but homoplasy is common. Similarly, obtuse basal angles appear to be plesiomorphic. Acute basal angles are usually produced posteriorly or laterally, conditions which are also derived. Again, homoplasy is expected. The bisinuate or biangulate pronotum with posterior gibbae is restricted to the inaequalis species group of *Microschatia,* which occurs in Baja California and extreme southern California. The function of the bigibbous prothorax is unknown, but a similar configuration occurs in *Stenomorpha tumidicollis* Blaisdell and *Trichiasida gibbicollis* (Horn), which also inhabit Baja California.

13. *Relative width of elytral base* (Fig. 6). Typically in Tenebrionidae the prothoracic and elytral bases are subequal. When the elytral base is notably narrower, the basal pronotal angles are often produced. Homoplasy may be expected in this feature.

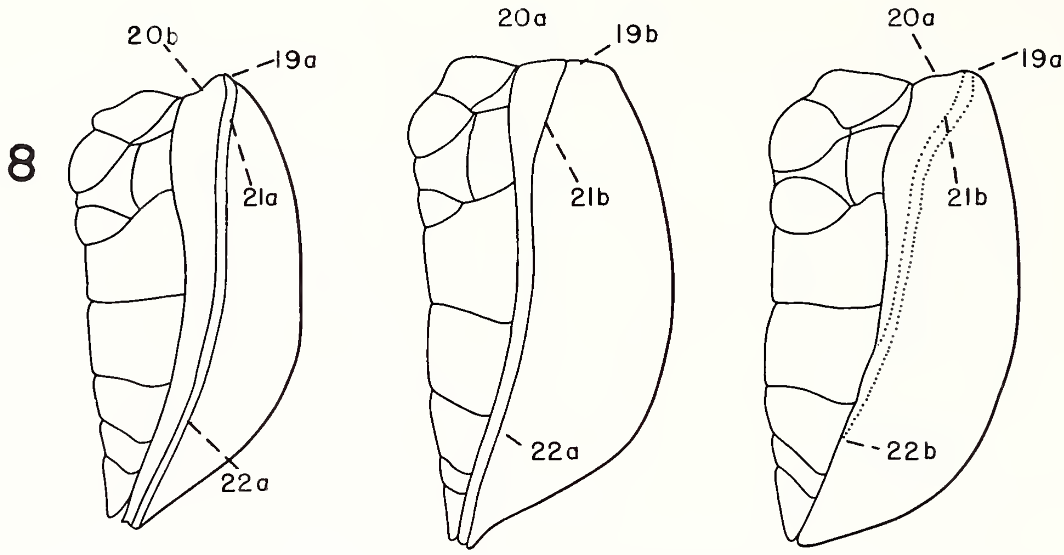


Fig. 8. Taxonomic characters of elytra and epipleura of *Microschatia rockefelleri* (left), *championi* (middle) and *solieri* right. Conventions as in Figures 1–5.

14. *Hypomeron sculpture.* This feature varies from smooth through punctate to tuberculate in Asidini and within *Microschatia,* making polarization problematic. Reversal of polarity of this character does not change the topology of the cladogram, however.

15. *Prosternal process.* In Asidini this structure is characteristically declivous immediately behind the procoxae and apically truncate or broadly rounded. In *Litasida* and *Bothrasida* it is porrect and broadly rounded, and in *Ucalegon,* porrect and sagittate (Fig. 7). The subhorizontal process of *Microschatia* is probably derived independently of the conditions described above. The sagittate condition is almost certainly apomorphic.

16. *Elytral shape.* See 9, above.

17–18. *Elytral sculpture.* Polarization is problematic. These characters have relatively low consistency indices and received the lowest assigned weights with successive weighting.

19–22. *Epipleural configuration* (Fig. 8). Typically in Tenebrionidae the epipleural carina is complete from the elytral humerus to the apex or nearly so, and subparallel with the elytral margin. In most Asidini the epipleural carina is visible only near the elytral apex and sometimes near the humerus. This apomorphic condition occurs in *Microschatia punctata, solieri* and *robusta.* In *M. rockefelleri, sulcipennis* and *morata* the epipleuron is very broad at the humerus, narrowing rapidly to about the level of the metacoxa, then narrowing gradually to the elytral apex. In all of these species the humeral angles are apomorphic in projecting forward and are slightly acute when viewed from below.

23–26. *Body setation and coating.* A large majority of Tenebrionidae, including most Asidini, have clean cuticle, without a coating of earth or detritus. Many Asidini, however, apparently secrete a material which cements fine particulate material to the body, often in characteristic patterns. Encrusting is an apomorphic feature which appears to have been derived many times in Asidini.

In addition to cuticular encrustations, some species of *Microschatia* have the typical hairlike setae apomorphically modified by slight to extreme flattening. The scaliform

setae may be evenly distributed or, in the apomorphic state, concentrated in particular areas on the head, thorax or elytra. White, slightly flattened setae on the legs are apomorphic to *punctata, solieri* and *robusta.*

27–31. These characters are all synapomorphies for *Microschatia.* Somewhat thickened tarsi occur in a few other genera (*Gonasida, Tisamenes*), but these are very different from *Microschatia* in other features, suggesting convergence. A very large mentum occurs in several other genera (*Sicharbas, Astrotus, Stenosides*), but these lack nearly all the other synapomorphies characterizing *Microschatia* and do not appear to be very closely related. The apical antennal segment is always reduced in Asidini, but only in *Sicharbas* and *Litasida* is the degree of reduction comparable to that in *Microschatia.* In *Sicharbas* the tenth segment is much enlarged with coalesced patches of tomentum. The very small eleventh segment is not amplected into a notch, as in *Microschatia.* These differences suggest independent reduction. The antennal apex of *Litasida* is essentially the same as that of *Microschatia.*

Results

A single most parsimonious tree of 48 steps (Fig. 9) was produced by HENNIG 86. The two main branches of the tree correspond to the punctata and inaequalis species groups (see below), which inhabit mainland Mexico and Baja California, respectively. The punctata species group and its two subgroups are each distinguished by at least six apomorphies (at least two of these unique). In contrast the inaequalis species group is distinguished by only two unique apomorphies and its subgroups by no more than one. The arrangement in Figure 9 conforms to our intuitive placement of taxa, except that *M. polita* is separated from *inaequalis,* which it resembles in general body shape. However, two derived features of cuticular sculpturing that are shared by *inaequalis, cedrosensis* and *costulata* are plesiomorphic in *polita* (characters 14, 17). The derived, sagittate prosternal process (character 15) is present in all members of the inaequalis group except *polita.*

Most of the homoplasy in Figure 9 is due to convergence, but two characters (no. 4 and 17) are each reversed once and two (18 and 21) are derived more than twice. These characters have a consistency index (Farris, 1989) of 0.33 and were given minimal weights (1 to 3) in successive weighting analyses. Characters 6, 7, 9, 10, 11, 13, 14, and 16 are each derived twice in Figure 9 (weights of 4). All the others are uniquely derived and given full weights of 10. The tree resulting from successive weighting is topologically identical to Figure 9, but the consistency index is 0.86 and the tree length is 267.

The cladistic structure in Figure 9 shows an obvious biogeographic pattern. The punctata species group inhabits the plateau of north central Mexico and adjoining southwestern United States. The inaequalis group species all occur in central to northern Baja California, with two species barely entering extreme southern California or Arizona and one (*polita*) apparently restricted to Arizona. Vicariance across the gulf of California also occurs in Coniontini (*Eusattus*) (Doyen, 1984), Triorophini (*Triphalopsis*: *Triphalopsoides*) (Doyen, 1990) and will probably be revealed by cladistic analyses in other Tenebrionidae such as *Argoporis* and *Eleodes.* Distributions of the individual species of *Microschatia* are inadequately known to reveal additional vicariance patterns.

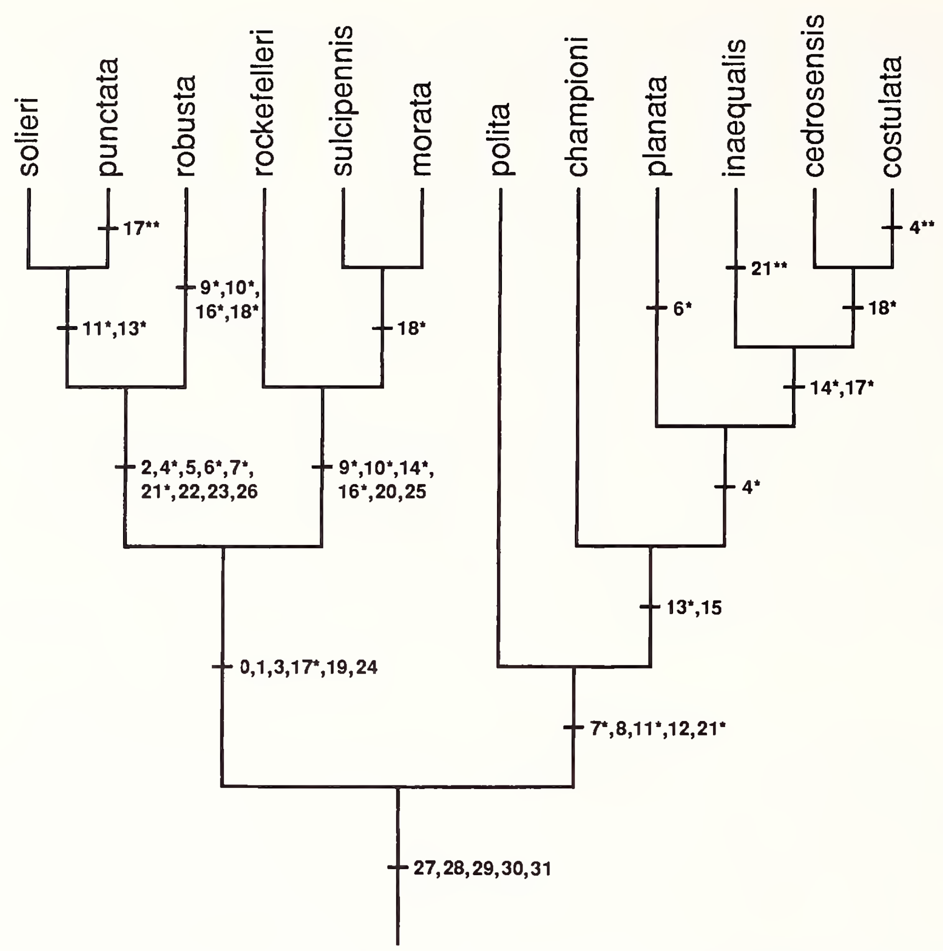


Fig. 9. Cladogram for species of *Microschatia*. Apomorphies are listed by character number for each branch. Single asterisks indicate character state convergences; double asterisks indicate reversals. Autapomorphies (other than reversals) are not shown. Characters and character states are described in Appendix 1 and discussed in the text. C.I. = 0.86.

Microschatia Solier

Microschatia Solier, 1836:474.
Pycnonotida Casey, 1912:89. NEW SYNONYMY.
Acroschatia Wilke, 1922:269. NEW SYNONYMY.

Description. Adult.—Strongly convex to somewhat flattened, robust beetles, often with flattened, scale-like setae on the dorsum.

Mentum transversely hexagonal to broadly cordate, closely contacting postgenal processes, exposing minute to moderate space at corners (Fig. 4); anterior border broadly emarginate, often with narrow, median notch. Gular pedestal broadly emarginate, almost as wide as base of mentum. Postgenal process extending to about basal third of mentum, apex broadly rounded. Ligula small, barely visible, rarely extending beyond emargination in mentum. Maxillary palps with apical segment isosceles or rectitriangular, similar in male and female. Labrum deeply, narrowly notched, broadly emarginate or entire; epistomum with anterior border arcuately emarginate. Eye very elongate oval or very weakly reniform, concealed when head is retracted; dorsal lobe slightly larger than ventral. Pronotum with lateral borders nearly evenly arcuate, flat or nearly so with margin sometimes thickened; base arcuate to bisinuate or biangulate, sometimes with paramedian basal gibbosities; posterior angles obtuse,

not overlapping elytral humeri to acute, projecting backward over humeri. Prosternal process broad, projecting posterad a short to moderate distance behind coxae, then abruptly declivous; apex subtruncate to sagittate, received in shallow to moderate mesosternal fossa. Elytra with variable sculpture; epipleuron broad and distinct at humerus, complete or becoming undefined at about first abdominal sternite. Anterior tibia cylindrical or flattened, with distinct spatulate or digitate process on outer apical angle; tibial spurs subequal or anterior spurs much larger than posterior. Tarsi thick, with short, stout spiniform setae beneath. Female reproductive tract typical of Asidini, with enlarged vagina, short, multiply-branched spermathecal tubes and long, distally enlarged spermathecal accessory gland (Figs. 10–11). Ovipositor with coxites straight or very weakly upcurved, about one-fourth length of paraprocts. Aedeagus with basal piece of tegmen about three-fourths to one times as long as paramere; paramere with apex acutely attenuate.

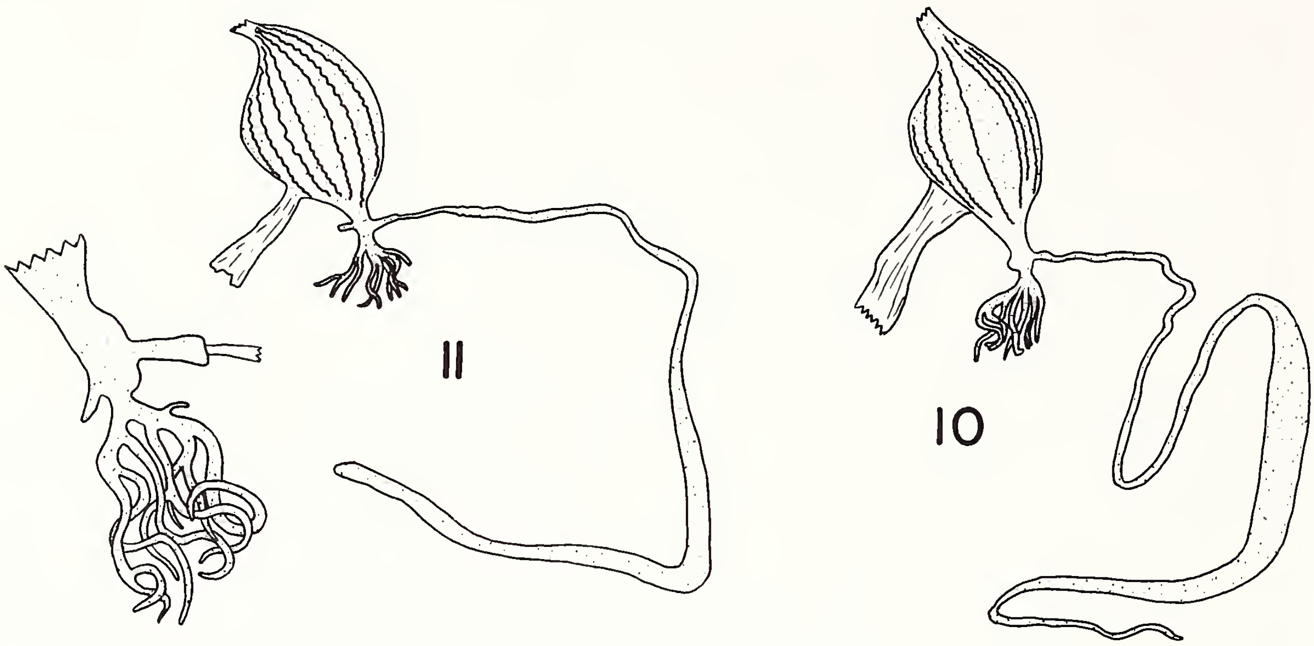
Late instar (Figs. 19–27).—Conforming to description of Asidini by Brown (1973) except for following features. Epicranial stem about one-third length of cranium; lateral epicranial sutures very short. Cranium with at least anterior one-third of dorsum covered by extremely short globular setae, appearing granular; genae densely covered with stout setae, these becoming longer, more slender ventrally. Clypeus with globular setae nearly contiguous in posterior half, glabrous anteriorly.

Prothorax with anterior and posterior borders lightly pigmented, granulate or not; mesothorax and metathorax subequal. Abdominal segments one to eight with anterior transverse band of setae; spiracles located about one-fourth to one-sixth distance from anterior margin, surrounded by sparse ring of setae. Abdominal segment nine expanded dorsoapically, conical to subconical in dorsal view; bearing fringe of long slender setae and dorsal covering of short, spinose setae; urogomphi absent. Prothoracic leg with trochanter, and femur bearing ventral patches of globular or coarse, spinose setae; tibia with comb of stout, spinose setae on ventral surface.

Type species.—*Microschatia punctata* Solier, 1836:475, monobasic. From his description it is evident that Solier examined a single specimen, which is the holotype. We have not examined the Solier type, but his original illustration and the distinctiveness of *punctata* leave little doubt as to its identity.

Discussion.—The configuration of the ventral mouthparts separates *Microschatia* from all other North American Asidini except *Sicharbas, Stenosides* and *Astrotus.* In these genera the mentum closely contacts the postgenal processes and the gula is nearly as broad as the buccal cavity so that only a small space, at most, is left at the posterior corners. In other genera the mentum usually does not contact the postgenal processes. The gula usually forms a pedestal that is narrower than the buccal opening, leaving relatively large spaces at the corners. In most *Microschatia* the epipleuron is broad and reaches the elytral humerus, whereas in *Sicharbus, Stenosides* and *Astrotus* the epipleuron is narrow from base to apex. This character also separates *Microschatia* from other North American Asidini except *Litasida,* in which there are large paragular spaces at the corners of the buccal cavity. Other features useful in distinguishing *Microschatia* are the relatively short, cylindriform antenna with thick flagellar segments enlarged gradually from base to apex; and the thick, cylindriform tarsi (also occurring in *Stenosides*; somewhat thickened in *Gonasida, Glyptasida*).

No clear-cut secondary sexual characters are known for any species of *Microschatia,* but most individuals may be sexed by examining the curvature of the abdomen in



Figs. 10, 11. Configuration of internal female reproductive tracts of *Microschatia sulcipennis* (left) and *robustus* (right). The inset shows the spermatheca of *sulcipennis.*

lateral silhouette. In females the abdomen is usually continuously convex from the metacoxae to the base of the fourth sternite, with sternites two and three distinctly bulging. In males sternites one and two are usually flat or slightly concave and sternite three bulges only slightly compared with four and five. Among species which have been collected in significant series, females average about 4% larger (as measured by abdominal length) than males in *solieri,* 8% larger in *planata,* 16% larger in *inaequalis* and 22% larger in *championi.* However, these averages, which are based on specimens collected at the same locality and year, are based on relatively small samples of seven to twelve individuals. Antennae of males are about 15 to 25% longer relative to head width than are those of females, and the penultimate segment tends to be relatively longer in males.

Larvae of *Microschatia* differ from those which have been associated with other genera of Asidini in the complete absence of urogomphi. Larvae of *Philolithus, Gonasida* and *Glyptasida* have the urogomphi reduced to minute tubercles (Brown, 1971, 1973). In others the urogomphi are distinct and often large (e.g., *Stenomorpha,* Brown, 1973).

Acroschatia Wilke (1922) was proposed as a subgenus to contain *M. robusta* Horn, which is very similar in all important characters to *punctata* (the genotype) and *solieri*; *sulcipennis, rockerfelleri* and *morata* differ principally in the more complete and evenly narrowing epipleural carina. If a natural division were to be recognized in *Microschatia* it would separate the mainland Mexican species from the Pacific coastal ones, and *Acroschatia* would remain a junior synonym of *Microschatia. Pycnonotida* Casey was erected to contain *M. inaequalis* (LeConte), another LeConte species and a number of new species, all of which we synonymize with *M. inaequalis.* Our analysis shows that *inaequalis* is very similar to other *Microschatia.* Therefore *Pycnonotida* is placed as a junior synonym of *Microschatia.* Since all 12 species clearly form a monophyletic lineage we have chosen to recognize a single genus and two species groups, defined as follows:

Characterization of the punctata species group.—Labrum deeply, narrowly emarginate; eye slightly constricted by epistomal canthus; antennal segment 10 with patches of sensory tomentum subequal; pronotum almost as wide as base at widest point; posterior surface evenly convex, never bigibbose; prosternal process broadly rounded; elytra with humeral angle projecting forward when viewed ventrally; body with some setae spatulate or scale-like; dorsum partially encrusted with soil.

The punctata species group includes *M. punctata, solieri, robusta, sulcipennis, rockefelleri* and *morata.* These species occur on the central plateau of Mexico from Hidalgo to Chihuahua and Coahuila, and in adjacent parts of Arizona, New Mexico and Texas, in subarid or seasonally arid woodland habitats.

Characterization of the inaequalis species group.—Labrum broadly, shallowly notched to subtruncate; eye relatively deeply constricted by epistomal canthus; antennal segment 10 with outer patch of sensory tomentum much larger than inner; pronotum much narrower at base than at widest point; posterior border bisinuate or biangulate, conforming to shape of prominent gibbae; prosternal process broadly rounded to sagittate; elytra with humeral angle projecting at nearly right angles to body axis when viewed ventrally; body setae uniformly slender, hairlike.

The inaequalis species group includes *M. inaequalis, polita, championi, planata, costulata* and *cedrosensis.* These species occupy subarid or arid chaparral, savannah woodland or desert habitats from extreme southern California to the Vizcaino region of Baja California.

In the following key the first part of the figure designations refers to the figure numbers; the second part refers to the character numbers from Appendix 1 and indicated in small font on the figures. Thus, Figure 6:9b indicates character 9, state b, illustrated in Figure 6.

KEY TO THE SPECIES OF *MICROSCHATIA*

1. Labrum deeply notched (Fig. 1:b); pronotum only slightly narrower across posterior angles than at middle (Fig. 6:9b) and lacking gibbosities on posterior border; body with at least some scaliform setae (punctata species group) 2

– Labrum emarginate, not notched (Fig. 1:a); pronotum notably narrower across posterior angles than at middle (Fig. 6:9a) and with pair of gibbosities on posterior border; body with only slender, hairlike setae (inaequalis species group) 7

2(1). Epipleural carina distinct from humerus to elytral apex (Fig. 8:22a); epipleuron narrowed more abruptly just behind humerus, then gradually to apex (Fig. 8:21b); antennal length more than 1.3 times head width; 10th antennal segment subquadrate (Fig. 5:7a) 3

– Epipleural carina becoming obliterated about one-half to two-thirds distance to elytral apex (Fig. 8:22b); epipleuron narrowed gradually from humerus to posterior termination (Fig. 8:21a); antennal length less than 1.2 times head width; 10th antennal segment wider than long (Fig. 5:7b) 5

3(2). Pronotal disk with marginal setae much larger, broader and denser than central, hairlike setae; disk never obscured by adherent soil or debris 4

– Pronotal disk with setae slender or flattened, but of similar shape and size over entire surface; disk often obscured by adherent soil or debris .... *morata* Horn

4(3). Elytra with three to six distinct rounded, shiny costae; intercostae dull, shagreened; pronotum with marginal band of white scales incomplete on anterior and posterior borders (Fig. 16) .... *sulcipennis* Horn

– Elytra confluently and densely punctate, ecostate or with one or two indistinct costae; pronotum with all borders covered with narrow zone of white scales (Fig. 15) . . . . *rockefelleri* Pallister
5(2). Elytral disk reticulate or coarsely punctatorugose (Figs. 13, 14); usually with weak costae evident 6
– Elytral disk densely covered with large, round, discrete punctures, confluent only laterally and on epipleuron; without evidence of costae (Fig. 12) . . . . . *punctata* Solier
6(5). Pronotum with broad, sharply defined marginal band of encrusted soil, leaving a smooth, subhexagonal central island with sparse punctures and irregular impunctate areas (Fig. 13); abdominal sternites with central impunctate areas . . . . *solieri,* new species
– Pronotum with narrow, indistinctly defined marginal band of encrusted soil; central area evenly, discretely and densely punctured (Fig. 14); abdominal sternites evenly punctate . . . . *robusta* Horn
7(1). Elytra distinctly and regularly costate (Figs. 31, 32) 8
– Elytra smooth, punctate or rugose, but without distinct costae (Figs. 33–35) 9
8(7). Pronotal disk with coarse, confluent punctures (Fig. 31) . . . . *cedrosensis,* new species
– Pronotal disk with fine, discrete punctures (Fig. 32) . . . . *costulata,* new species
9(7). Anterior and middle tibiae subclyindrical or elliptical in cross section; hind tibia usually straight; frons without tubercles 10
– Anterior and middle tibiae flattened, with outer margin carinate; hind tibia usually strongly sinuous; frons with tubercle at inner margin of eye . . . . *planata,* new species
10(9). Pronotal disk tuberculate; elytra coarsely rugose with overlay of fine tubercles (Fig. 33) . . . . *inaequalis* LeConte
– Pronotal disk finely to coarsely and confluently punctate; elytra punctate or punctatorugose 11
11(10). Body shiny; elytral punctures very small, sparse; posterior pronotal angles weak, obtuse (Fig. 34) . . . . *polita* Horn
– Body dull or with matte luster, not shiny; elytral punctures large, dense, often confluent; posterior pronotal angles strong, rectangular (Fig. 18) . . . *championi* Horn

Microschatia punctata Solier
(Fig. 12)

Microschatia punctata Solier, 1836:475; Champion, 1884:66.

Black beetles with coarsely, evenly punctate elytra; head, lateral margins of pronotal disk, hypomera, legs and elytral punctures coated with pale, extremely fine textured earth.

Female.—Head coated with soil; frons with scattered punctures, each bearing a short whitish or yellowish, slightly flattened, decumbent seta. Epistoma deeply emarginate anteriorly, lateral margin angulately indented at epistomal suture, which is shallow, obscure. Eye with slightly raised prominence at apex of dorsal lobe; constriction about one-fourth as wide as dorsal lobe. Antenna about as long as head width, all but third segment wider than long; moderately densely set with fine, pale setae; segment 2 less than half as long as segment 3; segment 10 slightly wider than long, asymmetrical; eleven nearly symmetrical. Mentum broadly emarginate with narrow, deep, medial notch. Ligula about one-third wider than notch in mentum, retractile, often scarcely visible. Postgenal process nearly right angled, with rounded apex. Gular pedestal deeply, angulately emarginate.

Pronotum widest slightly behind middle, three-fourths as wide across anterior

Fig. 12. *Microschatia punctata* Solier.

angles as basal; anterior angles slightly acute, posterior angles obtuse, scarcely extended posteriad; lateral margins thick, narrowly explanate; posterior margin biangulate, nearly straight medially; disk with scattered, coarse, deep to shallow, earth-filled punctures covering anterior quarter and narrow medial band or entire central portion of posterior two-thirds; slightly concave medially near posterior margin; lateral zones of disk caked with earth through which punctures with tiny, flattened, whitish setae are obscurely visible. Hypomeron solidly caked with earth through which few, scattered, pale setae project. Prosternum with sparse, deep, coarse, setiferous punctures, sometimes with impunctate longitudinal zone.

Elytra with base slightly narrower than base of thorax; disk covered with coarse,

discrete, earth-filled punctures larger than width of eye and separated by less than puncture width, becoming somewhat coalesced laterally. Epipleural carina indistinct in anterior third, not evident posteriorly; epipleuron rapidly narrowing from humerus to first sternite, then narrowing more gradually and disappearing. Abdominal sternites alutaceous with sparse, fine to moderately coarse setiferous punctures, especially laterally and on sternite five.

Femora finely punctate, partially covered with adherent earth; setae sparse, whitish, slightly flattened, decumbent. Middle and hind tibia subcylindrical, covered with adherent earth and sparse mixture of short, coarse, suberect brownish spines and whitish, slightly flattened, decumbent setae; anterior tibia with fine setae anterodorsally, spines ventrally; tarsi mostly setose dorsally, mostly spinose ventrally.

Male.—Differs as indicated in generic description.

Measurements.—Pronotal length 4.6 to 5.4 mm; greatest pronotal width, 6.5 to 7.7 mm; elytral length 10.0 to 12.8 mm; greatest elytral width 8.0 to 9.8 mm.

Type.—Not examined. Solier's description is based on a single individual, which is the holotype. The identity of *punctata* is clear from the description and accompanying illustration.

Type locality.—Mexico.

Diagnosis.—*Microschatia punctata* is most similar to *M. solieri* Brown and Doyen. In *punctata* the elytral depressions are round, subequal in size, and rarely coalesced on the disk. They are evenly distributed, without trace of longitudinal ridges. In *solieri* the depressions are round to very irregular in shape and often coalesced, producing a rugose appearance. Areas without depressions form three very weakly elevated longitudinal ridges extending onto the declivity.

Distribution.—Queretaro, Mexico.

Material examined.—Mexico, no additional data (1); F. Bates (1); Sallé Collection (1); Queretaro, 1 mi N Peña Blanca, IX-13-1970, (1).

Microschatia solieri, new species
(Fig. 13)

Microschatia punctata, Champion, 1892:503; Horn, 1893:140; Casey, 1912:94.

Black beetles with rugose, subcostate elytra; head, lateral margins of pronotal disk, hypomera, legs and elytral depressions coated with pale, extremely fine textured earth.

Female.—Very similar to *M. punctata* Solier, except for following features: pronotal disk with lateral, earth coated zone usually extending at least partway along posterior margin. Elytral disk with round to very irregular, earth coated depressions, producing rugose appearance. Elevations between depressions more-or-less coalesced into sutural and two paramedial ridges, producing subcostate appearance in most individuals. Abdominal sternites with discrete bands of earth coating lateral fifths.

Male.—Differs as indicated in generic description.

Measurements.—Pronotal length 4.7 to 5.5 mm; greatest pronotal width 6.7 to 7.5 mm; elytral length 10.2 to 12.7 mm; greatest elytral width 7.6 to 9.4 mm.

Holotype female (OSU) and 5 female, 3 male paratypes from Mexico, Hidalgo, 2 mi SE Zimapan, VI-24-1975, L. E. Watrous. Additional paratypes (sex not determined) from Hidalgo, as follows: Ixmiquilpan, XI-12-1946, P. E. Skinner (2); VI-1963, F. D. Bennett (1); Ixmiquilpan, 10 mi N, 7,000′, VI-22-1982, R. L. Aalbu; 7

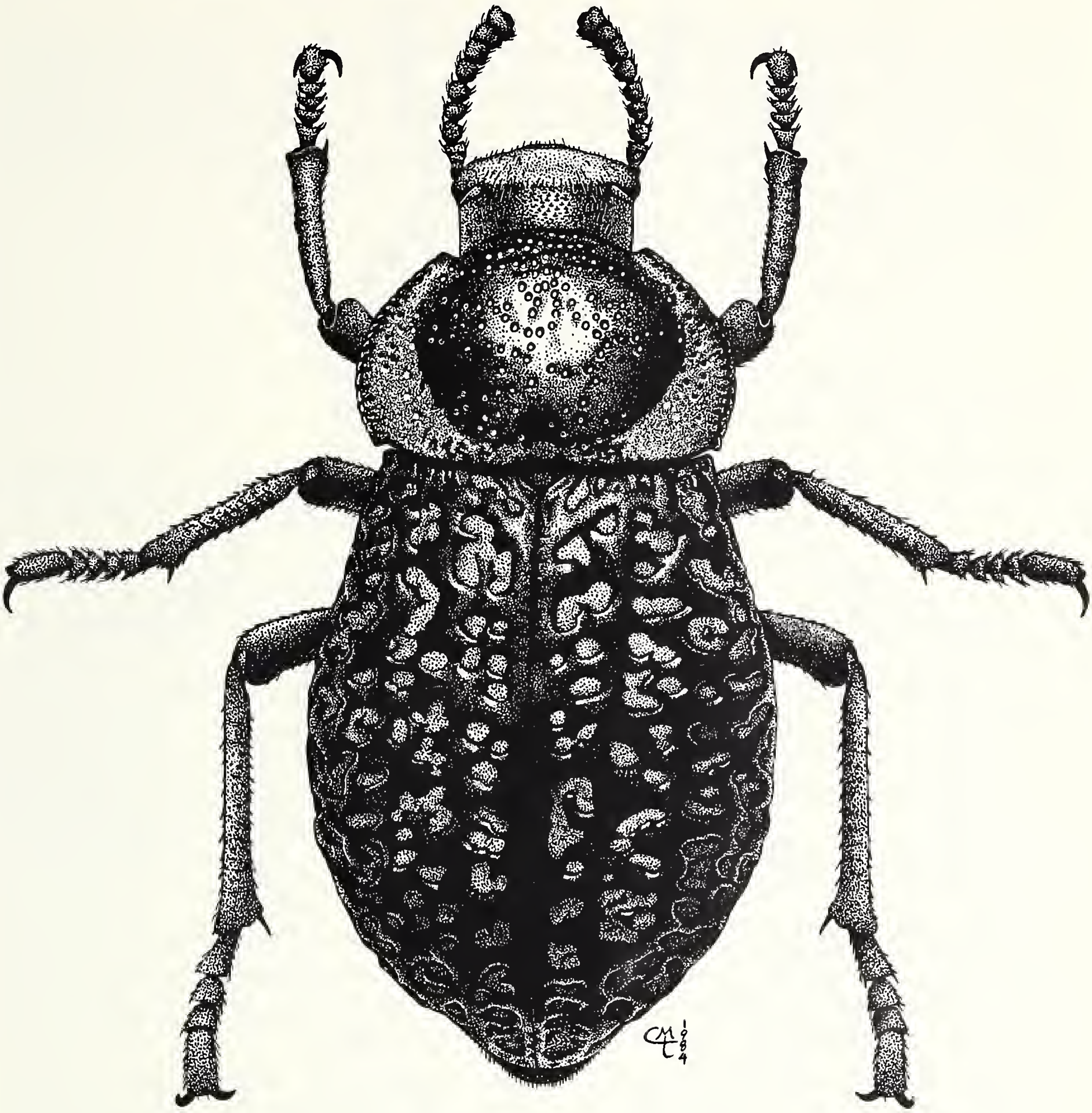


Fig. 13. *Microschatia solieri* Brown and Doyen.

mi W Pachuca, VI-24-1975, L. E. Watrous (4); El Tablon, 7 mi SW Zimapan, VIII-19-1964, J. and W. Ivie (6); 2 mi N Tasquillo, Rio Tula, 5,300′, VI-28-1965, N. Chornoff (2); Zimapan, Hoge (15); Zimapan, VI-11/14-1951, P. D. Hurd (1); Zimapan, 2 mi SE, VI-24-1975, C. A. and B. W. Triplehorn, L. Watrous, Q. D. Wheeler (5). Zimapan, 3 mi S, VI-25-1971, Ward and Brothers (1).

Diagnosis.—*Microschatia solieri* is most similar to *M. punctata* Solier, under which the differences are enumerated. It also resembles *M. robusta* Horn, but in *solieri* the pronotal disk is laterally impunctate or finely, obscurely punctate, usually with irregular impunctate central areas as well (entire disk uniformly, coarsely punctate in *robusta*). In *solieri* the posterior pronotal angles are slightly produced posterad and appear obtuse or nearly right-angled; the disk bears a broad medial depression near the posterior border. In *robusta* the posterior pronotal angles are strongly produced

and acute; the disk is evenly convex across the posterior quarter. The elytra of *solieri* have many strong, transverse ridges connecting the lateral ones. In *robusta* the transverse ridges are much finer than the longitudinal ones and often do not connect adjacent ridges. Examination of specimens in the British Museum from Zimapan identified as *M. punctata* by Champion showed that they are *solieri*, not *punctata*. These were briefly described as "var." by Champion (1892:503).

Distribution.—Hidalgo, Mexico.

Microschatia robusta Horn
(Fig. 14)

Microschatia robusta Horn, 1893:142; Pallister, 1954:14.
Acroschatia robusta, Wilke, 1922:269.

Black beetles with subcostate to costate, weakly reticulate elytra; head, pronotal punctures, hypomera, elytral depressions and legs coated with pale, extremely fine-textured soil.

Female.—Similar to *M. punctata* Solier, except for following features: pronotum three-fifths as wide across anterior angles as posterior; anterior angles about 90°, posterior angles acute, strongly produced posterad; lateral margins thick, narrowly explanate, upturned; posterior margin arcuate between posterior prominences, slightly flattened medially. Disk uniformly covered with coarse, shallow, contiguous or subcontiguous, minutely setiferous punctures filled with earth; evenly convex across posterior quarter, or very weakly concave in middle. Hypomeron solidly caked with earth, largely obscuring sparse setiferous punctures. Prosternum tuberculately punctate anterolaterally; with sparse, coarse, setiferous punctures medially and on prosternal process.

Elytral base equal in width to base of thorax with humeri projecting prominently forward, bearing slight indentation for posterior pronotal angles; disk with sutural and two paramedial costae interconnected by finer, raised reticulations; depressions coated with earth through which project sparse, flattened, minute, whitish setae. Abdominal sternites with anterolateral quadrants coated with earth. Femora finely, shallowly punctate, punctures filled with earth, or anterior femora solidly coated.

Male.—Differs as indicated in generic description.

Measurements.—Pronotal length 4.0 to 4.8 mm; greatest pronotal width 6.3 to 7.5 mm; elytral length 8.7 to 12.0 mm; greatest elytral width 7.0 to 9.1 mm.

Holotype.—Museum of Comparative Zoology, Harvard University, sex not determined.

Type locality.—Mexico, Coahuila.

Diagnosis.—*Microschatia robusta* is similar to *M. solieri* Brown and Doyen. Differences are detailed under the latter. It is similar in most characters to *M. punctata* Solier, but is easily separated by the prominent posterior pronotal angles and reticulately sculptured elytra (pronotal angles scarcely produced; elytra coarsely punctate in *punctata*).

Pallister (1954) believed *robusta* to be very closely related to *morata* Horn, stating that it would probably eventually prove to be the same species. However, *robusta*, *punctata* and *solieri* are clearly related by the abruptly narrowed epipleuron, by the

Fig. 14. *Microschatia robusta* Horn.

well developed earthen coating of the body and by the presence of pale setae on both dorsum and venter, including the femora. In contast, in *morata, sulcipennis* and *rockefelleri,* the epipleuron narrows continuously and the earthen coating is scant, whereas the peripheries of the pronotal and elytral disks are thickly lined with whitish scales (always absent in the *punctata* group). The body and leg setae of the *morata* group are uniformly dark colored. Additional synapomorphies and differences between each group are specified on Figure 9.

Distribution.—Northeastern Mexico and extreme southeastern Texas.

Material examined.—Texas, Cameron County, Brownsville, IV-27-1962, intercepted with cactus (1); Kleberg County, Kingsville (1). Mexico, Neuvo Leon, Las Margaritas, VIII-11-1965 (4) 29 km N San Cayetano de las Vacas, V-31-1981 (1). Tamaulipas, Condalia (1).

Microschatia rockefelleri Pallister
(Fig. 15)

Microschatia rockefelleri Pallister, 1954:15.

Black beetles with pronotum, lateral edges of elytra and posterior third of medial elytral suture highlighted with white scales.

Female.—Head not coated with earth; dorsum with hemicircle of dense, blunt tipped, white scales running from lateral epistomal sutures, between eyes and just before pronotal margin; central part of frons with punctures much sparser, bearing slender brownish or blackish setae, sometimes with few white scales intermingled. Epistoma shallowly emarginate anteriorly, angulately indented at epistomal sutures. Eye with slight to moderate prominence at apex of dorsal lobe; constriction about one-fifth as wide as dorsal lobe. Antennal length about one and one-fourth times head width; segments four to seven slightly longer than wide; eight subquadrate; nine wider than long; ten subquadrate, almost symmetrical; eleven nearly symmetrical; all segments set with moderately dense, coarse, black setae. Mentum set with coarsely setiferous punctures; broadly emarginate with shallow medial notch. Ligula almost twice as wide as notch, small but always visible. Postgenal process nearly right-angled with rounded apex. Gular pedestal arcuately to angulately emarginate.

Pronotum widest slightly behind middle, three-fifths as wide across anterior angles as basal; anterior angles slightly acute with rounded apex; posterior angles acute, distinctly produced posterad; lateral margins thick, very narrowly explanate; posterior margin arcuate between posterior prominences. Disk uniformly convex; borders narrowly covered by contiguous or overlapping, blunt tipped, white scales; central seven-eighths more sparsely set with setigerous punctures; setae either slender, flattened or a mixture, either brownish or whitish. Hypomeron sparsely set with fine punctures supertended by short, coarse setae. Prosternum tuberculopunctate laterally, becoming setiferously punctate medially and on process. Prosternal process broadly rounded.

Elytral base subequal to thoracic base; disk rugose; depressions shagreened, lightly coated with earth; ridges black, epipleural margin and posterior one-fourth to one-third of sutural margin narrowly lined with dense, blunt tipped, white scales; central areas sparsely covered with sparse, brownish, somewhat flattened setae. Epipleural carina distinct; epipleuron asperate, gradually narrowing from base to elytral apex. Abdominal sternites uniformly, moderately densely set with setiferous punctures; setae slender, brown.

Femora moderately densely set with setiferous punctures; setae black, declined. Middle and hind tibia moderately densely covered by mixture of black setae and shorter, coarser, black spines; anterior tibia subcylindrical with setae anteriorly, setae and spines posteriorly. Tarsi setose dorsally, mostly spinose ventrally.

Male.—Differs as indicated in generic description.

Measurements.—Pronotal length 4.5 to 4.9 mm; greatest pronotal width 6.6 to 7.5 mm; elytral length 9.5 to 12.3 mm; greatest elytral width 7.4 to 8.8 mm.

Holotype male.—American Museum of Natural History, New York.

Type locality.—Mexico, Chihuahua, 25 mi SW Camargo.

Diagnosis.—The fringe of white scales bordering the pronotal and elytral disks distinguishes *M. rockefelleri* from all other species except *morata* Horn and *sulci-*

Fig. 15. *Microschatia rockefelleri* Pallister.

pennis LeConte. In *morata* there is occasionally an indistinct fringe of whitish scales on the elytra. However, the thorax and head of *morata* are uniformly sparsely covered by slightly flattened setae, contrasting with the distinct patterning of *rockefelleri.* In addition, each elytron of *morata* bears three narrow, uneven longitudinal carinae; the elytra of *rockefelleri* are uniformly rugose, with only a faint indication of longitudinal pattern in some individuals.

In *sulcipennis* the elytra each bear a sutural and three to five distinct discal costae. The intercostal areas are shagreened, without the coating of earth characteristic of *rockefelleri.* In *sulcipennis* the fringe of white setae is narrower than in *rockefelleri* and is usually incomplete on the anterior and posterior margins.

Distribution.—Durango and Chihuahua, Mexico.

Material examined.—Mexico, Chihuahua, 17 mi SE Ciudad Camargo, VII-30-

1974 (1); 42 mi SW Camargo, 4,900′, VII-15-1947 (2); Ciudad Jimenez, 21 mi SE, VII-8-1986, 4,720′ (2); Ciudad Jimenez, 10 mi N, VII-17-1969 (1); Hidalgo de Parral, 5,500′, VII-17-1947 (1); VII-31-1959 (1). Durango, 4 mi S Casco, VI-16-1960, 5,800′ (2); 2 mi NW Nombre de Dios, VII-31-1959, 5,500′ (1).

Microschatia sulcipennis LeConte
(Fig. 16)

Microschatia sulcipennis LeConte, 1858:18; Horn, 1870:282; 1893:142.

Black beetles with sulcate elytra and narrow, obscure fringes of whitish scales around margins of pronotum and elytra.

Female.—Body usually lacking coating of soil. Head with sparse band of punctures bearing blunt-tipped, whitish scales running from each epistomal suture to prominence above eye, sometimes continuing briefly mesad, but always broadly interrupted across vertex. Central part of frons with punctures much sparser, bearing slender or slightly flattened blackish or brownish setae. Epistoma shallowly emarginate anteriorly, angulately indented at epistomal sutures. Eye with slight prominence at apex of dorsal lobe; constriction about one-fourth as wide as dorsal lobe. Antennal length about one and one-third times head width; segments four to eight slightly longer than wide; nine and ten subquadrate, ten and eleven almost symmeterical; all segments set with moderately dense, coarse, black setae. Mentum broadly emarginate with shallow, V-shaped to arcuate medial notch. Ligula almost twice as broad as notch, small but visible. Postgenal process nearly right angled or obtuse, apex broadly rounded. Gular pedestal shallowly, angulately or arcuately emarginate.

Pronotum widest slightly behind middle, slightly more than one-half as wide across anterior angles as basal; anterior angles slightly acute with rounded apex; posterior angles acute, distinctly produced posterad; lateral margins thick, very narrowly explanate; posterior margin arcuate between lateral prominences. Disk uniformly convex; lateral borders margined by narrow zone of contiguous or subcontiguous white, blunt tipped scales; anterior and posterior borders with scales lacking or attenuating medially, never continuous; central nine-tenths more sparsely set with setigerous punctures; setae slightly flattened, brownish or blackish. Hypomeron and prosternum as in *rockefelleri.*

Elytral base narrower than thoracic base; disk with sutural and five lateral costae on each side, alternately weaker and stronger; costae weakly interconnected by irregular transverse elevations, producing a somewhat rugose appearance in some individuals; entire surface shagreened, dull; epipleural margin very narrowly lined with whitish or yellowish, blunt-tipped scales, sometimes interrupted or disappearing posteriorly; suture sometimes with short row of whitish scales near apex. Epipleural carina distinct; epipleuron asperate, gradually narrowing from base to elytral apex. Abdominal sternites very finely, uniformly and moderately densely set with minutely setiferous punctures; setae brownish. Legs as in *rockefelleri.*

Male.—Differs as indicated in generic description.

Measurements.—Pronotal length 4.3 to 5.0 mm; greatest pronotal width 6.3 to 7.5 mm; elytral length 9.9 to 11.7 mm; greatest elytral width 7.0 to 8.6 mm.

Holotype (sex not determined).—Museum of Comparative Zoology, Harvard University.

Fig. 16. *Microschatia sulcipennis* LeConte.

Type locality.—Texas, Llano Estacado.

Diagnosis.—*Microschatia sulcipennis* is most similar to *rockefelleri* Pallister. Differences are detailed under the latter. Some individuals of *M. morata* have a narrow border of whitish or yellowish setae on the lateral elytral margins. The setae, however, are only slightly flattened and much less scale-like than in *sulcipennis* or *rockefelleri*. The pronotal disk of *morata* is never set off with a border of white scales. In addition, in *sulcipennis* each elytron bears six quite rectilinear costae. In *morata* each elytron has three discal and a weak sutural carinae, which are sinuous and much narrower than those of *sulcipennis*.

Distribution.—Western Texas. No records are known for adjacent parts of New Mexico or Mexico.

Material examined.—Texas, Big Bend, VI-1965 (1); Brewster County, Big Bend National Park, Chisos Mountains, The Basin, 5,400', VIII-14-1948 (2); 4,000', V-27-1952 (2); VIII-1-1973 (2); Green Valley, VII-20 (2). Culberson County, Frijole, VII-15-1933 (1); Guadalupe Mountains National Park, VII-17-1974 (1); Pine Springs, VII-12-1928 (3); 2 mi NW Pine Springs, VIII-14-1965 (2).

Microschatia morata Horn
(Fig. 17)

Microschatia morata Horn, 1878:56; 1893:141.

Black beetles, sometimes appearing brown or blackish brown because of adhering earth; elytra each with three somewhat sinuous, narrow, rounded carinae.

Female.—Head not coated or with very light coating of earth; dorsum with setiferous punctures, sparse on frons, becoming denser near eyes and lateral epistomal sutures; setae flattened, pointed, yellowish or whitish on frons, becoming slender, hairlike on epistomal margin. Epistoma moderately, arcuately emarginate anteriorly, angulately indented at epistomal sutures. Eye with slight to moderate prominence at apex of dorsal lobe; constriction about one-fourth to one-fifth as wide as dorsal lobe. Antennal length about one and one-fourth times head width; segments four to seven subquadrate, eight and nine wider than long; ten subquadrate, nearly symmetrical with tomentose sensory patches subequal; eleven nearly symmetrical; all segments set with moderately dense, coarse, black setae. Mentum broadly emarginate with shallow medial notch. Ligula almost twice as broad as notch, small but exposed. Postgenal process nearly right angled with rounded apex. Gular pedestal angulately emarginate.

Pronotum widest about three-fourths distance from apex to base; slightly more than one-half as wide across anterior angles as basal; anterior angles slightly acute with rounded apex; posterior angles approximately right angled or slightly acute, slightly to moderately produced posterad; lateral margins thick, very narrowly explanate; posterior margin arcuate or very weakly bisinuate between lateral prominences. Disk uniformly convex; coarsely, shallowly and contiguously to confluently set with setiferous punctures; central area with few slightly raised, very irregular, anastomosing ridges, producing rugose appearance; setae flattened, yellowish or whitish, pointed in central part of disk, sometimes with blunt tips peripherally. Hypomeron sparsely set with punctures bearing flattened, yellowish or whitish setae; prosternum with flattened setae laterally; spinose, dark setae medially and on process. Elytral base wider than or subequal to thoracic base; disk with weak sutural and three stronger lateral costae on each side; costae narrow, rounded, somewhat sinuous and occasionally interconnected by irregular, sinuous transverse ridges, giving sparsely rugose appearance; costae and ridges shiny black; depressions shagreened, dull, very sparsely set with slender brownish or blackish setae; epipleural margin of each elytron sparsely lined with irregular, occasionally interrupted row of whitish, flattened, blunt-tipped setae; similar setae sometimes forming very narrow row along posterior third of suture. Epipleural carina distinct; epipleuron asperate, gradually narrowing from base to apex. Abdominal sternites uniformly, moderately densely set with setiferous punctures; setae slender, brownish or blackish. Legs as in *rockefelleri*.

Fig. 17. *Microschatia morata* Horn.

Male.—Differs as indicated in generic description.

Measurements.—Pronotal length 3.1 to 4.5 mm; greatest pronotal width 4.9 to 6.5 mm; elytral length 8.6 to 10.6 mm; greatest elytral width 5.9 to 8.3 mm.

Holotype (sex not determined).—Museum of Comparative Zoology, Harvard University.

Type locality.—Grant County, New Mexico.

Diagnosis.—*Microschatia morata* is similar to *sulcipennis* LeConte and *rockefelleri* Pallister in having the elytra margined with white, scale-like setae. In the last two species the setae are almost as broad as long, with very blunt, almost truncate apices. In *morata* the setae (as well as those on the thoracic margins) are distinctly longer than broad, with the apices rounded (usually pointed on the thorax). Additional differences are detailed under the other two species.

Distribution.—Southeastern Arizona, southwestern New Mexico south to Durango, Mexico.

Material examined.—Arizona, Cochise County, VII-23-1908 (1); no date (1); Chiricahua Mountains (1); Chiricahua Mountains, VII-22-1961 (1); VII-30-1963 (1);

Huachuca Mountains (3); VII-18-1938 (1); Miller Canyon, VI-4-1982 (1); VII-10 (1); VII-21 (1); VII-22-1981 (1); Ramsey Canyon, VII-19-1912 (1); Palmer Lee, VII-13-1907 (5); VII-27-1907 (1). Santa Cruz County, Mount Washington [near Nogales], 6,000′, VII-13-1919 (1). New Mexico, no additional data (2); Catron County, Luna, VIII-31-1935 (1). Doña Ana County, 8 mi E Las Cruces, 5,700′, VII-19-1973 (1). Socorro County, Magdalena (1). Mexico. Chihuahua, Madera, 12.6 mi S, VII-6-1986, 7,500′ (1); Primavera, 5,500–6,000′, VI-30-1947 (1); Santa Barbara, 6,200′, II-17-1947 (1); IV-24-1947 (1); V-10-1947 (1); La Sauceda, 7,000′, VII-21-1947 (1). Durango, 4 mi NNE Boquilla, 6,200′, VII-15-1960 (1). Sonora, Minas Nuevas, VII-7-1952 (3).

Microschatia championi Horn
(Fig. 18)

Microschatia punctata Horn, 1870:282 (not Solier, 1836).
Microschatia championi Horn, 1893:140.

Black beetles with finely to coarsely punctate pronotum and coarsely to very coarsely punctate or punctatorugose elytra.

Female.—Frons and epistoma with dual punctation; coarser, setiferous punctures several times diameter of eye facets; finer punctures much smaller than eye facets, not appearing setiferous. Epistoma shallowly, arcuately emarginate anteriorly, scarcely indented at epistomal sutures. Eyes without prominence at apex of dorsal lobe; constriction slightly more than one-third as wide as dorsal lobe. Antennal length about one and one-fourth times head width; segments four to seven slightly longer than wide, eight subquadrate, nine and ten wider than long; ten asymmetrical, with outer half larger; eleven strongly asymmetrical; segments two to ten set with moderately dense, coarse black setae; eleven with setae only on inner angle. Mentum broadly, very shallowly emarginate with shallow median notch. Ligula almost twice as broad as notch, always exposed. Postgenal process obtuse with broadly rounded apex. Gular pedestal slightly to moderately emarginate.

Pronotum widest at middle or slightly before, then distinctly constricted to base; about three-fifths as wide across anterior angles as basal; anterior angles nearly right angled with broadly rounded apex; posterior angles nearly right angled, not produced posterad; lateral margins thick, moderately explanate; posterior margin biangulate, with middle part almost twice width of lateral parts. Disk shallowly and sparsely punctate with punctatorugose lateral zones to deeply and coarsely or confluently punctate over entire surface; punctures minutely setiferous. Hypomeron nearly impunctate to deeply, coarsely punctate. Prosternum finely to coarsely punctatotuberculate laterally, becoming coarsely punctate or punctatorugose medially and on process; process narrowly rounded or sagittate.

Elytral base wider than or subequal to thoracic base; disk with sparse punctures slightly larger than those of thorax and arranged in rows medially, becoming more coarsely, densely and irregularly punctate laterally and punctatorugose near epipleuron or occasionally punctatorugose or rugose throughout. Epipleural carina fine, distinct from humerus to elytral apex; epipleuron smooth to rugulose, abruptly narrowing posterad of humerus, then gradually to apex. Abdominal sternites uniformly,

Fig. 18. *Microschatia championi* Horn.

moderately densely set with fine to coarse, minutely setiferous punctures; setae blackish. Legs as in *rockefelleri.*

Male.—Differs as indicated in generic description.

Measurements.—Pronotal length, 4.5 to 5.6 mm; greatest pronotal width 6.3 to 8.6 mm; elytral length 10.5 to 14.5 mm; greatest elytral width 7.7 to 10.7 mm.

Lectotype (sex not determined).—Museum of Comparative Zoology, Harvard University.

Type locality.—Peninsula of lower California.

Diagnosis.—In general appearance *Microschatia championi* is similar to *cedrosensis* Brown and Doyen and *costulata* Brown and Doyen. However, *championi* has the elytra punctate or rugose, while the other two have distinctly costate elytra. In addition both *cedrosensis* and *costulata* are more slender and elongate (elytral length/width = 1.49 to 1.53) than *championi* (elytral length/width = 1.24 to 1.45).

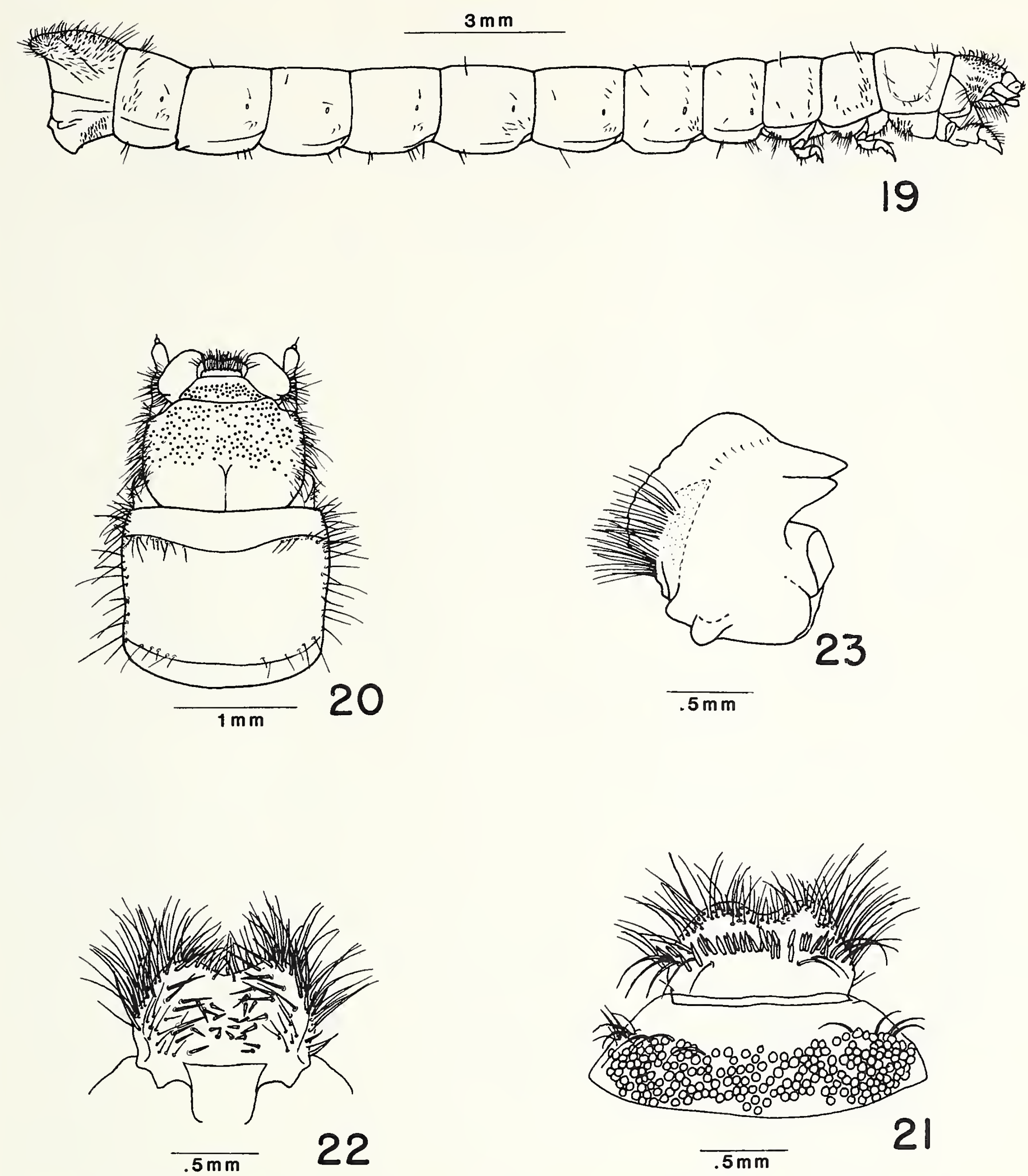
Variation.—Five individuals have very coarsely punctate pronota and coarsely punctate or punctatorugose elytra, in contrast to the finer sculpturing usually encountered. All of these individuals are from relatively low elevations (0 to 100 m) in the northern (San Quintin) and southern (25 mi N Guerrero Negro; El Arco; Juanito Cove, 33 mi N Loreto) parts of this species' range. However, the few other individuals known from these areas (San Telmo, Santa Rosa in the north; near Punta Prieta in the south) have the typically finer sculpturing. The few specimens from southern California do not vary significantly from typical individuals in the central part of the range.

Distribution and habitat.—Extreme southern California to Loreto, Baja California Sur. A single specimen from the University of Arizona collection is labeled from Organ Pipe Cactus National Monument, Pima County (see material examined). This locality is so removed from the documented range of *M. championi,* that it should be regarded as questionable until verified by additional collections.

Relatively large collections of *M. championi* have been made along Arroyo Catavina in the vicinity of the Rancho Santa Ynez, Baja California Norte. This is an uplifted (about 500 to 700 m elevation), granitic region with palm oases situated in ravines with permanent surface or subsurface water. The beetles occur in the relatively moist, sandy areas about the oases, where they are active crepuscularly. Another tenebrionid, *Eusattus catavinus,* is narrowly endemic to this uplifted area of palm oases (Doyen, 1984:46).

Material examined.—United States. Arizona, Pima County, Organ Pipe Cactus Nat. Mon., Ajo Mtns, Alamo Canyon, XII-17-1980 (1). California, Imperial County, Colorado Desert, I-14-1950 (1); Davies Valley, II-22-1970 (1); Mountain Springs, IV-4-1930 (1) III-27-1979 (1). Mexico. Baja California Norte, Agua de Refugio, IV-1-1935 (1); El Arco, I-20-1965 (1); Arroyo Catavina, 35 mi S El Progresso, IV-2-1976 (29); 2.5 mi NW Catavina, VII-13-1979 (1); 5 mi N, 1 mi W Catavina, IV-5-1981 (1); 10 mi N Catavina, IV-4-1977 (1); 25 mi N Guerrero Negro, I-20-1972 (2); 5 mi N Punta Prieta, IX-5-1951 (1); 20 mi N Punta Prieta, III-29-1973 (1); 38 mi S Punta Prieta, III-27-1935 (1); Rancho Santa Ynez, I-3-1977 (1); 2 mi N Rancho Santa Ynez, III-27-1973 (3); 6 km NW Rancho Santa Ynez, 1,800′, I-1976 (23); 9 km NW Rancho Ynez, 550 m, IV-4/30-1978 (15); inland from San Quintin, V-26-1956 (1); 5 mi W San Telmo, I-9-1976 (1); Santa Rosa (no date) (1); 1 mi N El Socorro, III-25-1973 (1). Baja California Sur, San Juanito Cove, 33 mi N Loreto, XII-24/26-1986 (1); 7 km N Rancho Tablon (27°37′N, 113°21′W), 130 m, I-1-1982 (2).

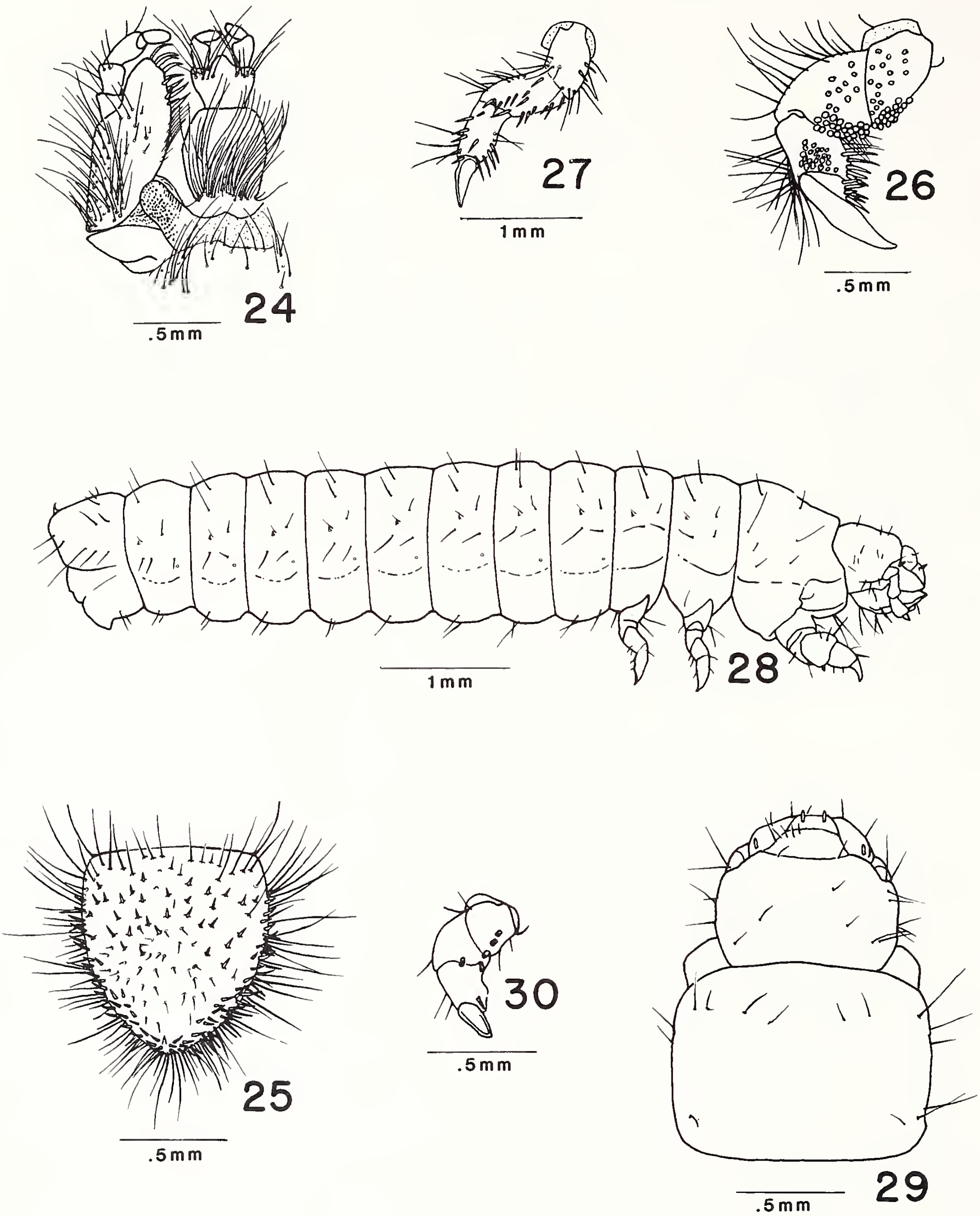
Description of late instar larva (Figs. 19–30). Length 36–42 mm; head capsule width 2.7–3.5 mm; five specimens, probably representing two instars, according to head capsule widths; semicylindrical dorsally, flattened ventrally; pale creamy white



Figs. 19–23. Structures of late instar larva of *Microschatia championi.* 19. Lateral aspect of larva. 20. Dorsal aspect of head and pronotum. 21. Dorsal aspect of clypeus and labrum. 22. Epipharynx. 23. Dorsal aspect of left mandible.

to yellow, except for dark claws, mandibular apices, oral rim and cuticular granules on head and legs.

Cranium densely granulate over anterior two-thirds of dorsum (Fig. 20), sparsely set with posteriorly declined setae about half-length of second antennal segment (not shown in Fig. 20), these arising between granules; genae densely set with stout setae about as long as second antennal segment, becoming longer, more slender ventrolaterally and in paragular region. Clypeus (Fig. 21) with nearly contiguous granules in posterior half, few setae laterally, glabrous anteriorly. Labrum with irregular transverse median row of flattened spines about half length of second antennal segment;



Figs. 24–29. Structures of larval *Microschatia championi.* 24. Maxillolabium of late instar. 25. Dorsal aspect of ninth abdominal tergite of late instar. 26. Posterior aspect of foreleg of late instar. 27. Posterior aspect of mesothoracic leg of late instar. 28. Lateral aspect of first instar larva. 29. Dorsal aspect of head and pronotum of first instar. 30. Foreleg of first instar.

anterior margin with longer, slender setae (Fig. 21); epipharynx with stout tormal arms; epipharyngeal setae stouter medially, in confused array (Fig. 22). Antenna with second segment slightly shorter than first; third segment papillate. Mandibles (Fig. 23) with prominent preapical gibbosity, more abruptly developed on right; left mandible with small, blunt, preapical tooth on dorsal margin. Maxilla with proxicardo

leathery, finely granulose; disticardo sclerotized, glabrous; mala with fine, long setae on lateral basal two-thirds of outer surface (Fig. 24); inner margin with double row of stout spines, becoming longer and curved apically, becoming slender, hairlike basally. Mentum with dense, long projecting setae in posterior half, glabrous anteriorly (Fig. 24); prementum sclerotized, with brush of long setae near anterior corners; hypopharyngeal sclerome with molar surface subovoid in anterior aspect, shallowly excavate, without distinct cusps; ligular surface with numerous long, slender, anterodorsally directed setae. Submentum asetose, covered with fine granules; gula sclerotized, with numerous long setae.

Prothorax (Figs. 19, 20) with anterior sixth, posterior eighth and anterior half of lateral margins very finely granulose, appearing pigmented; granulose anterior and posterior regions subtended by rows of sparse, fine setae, these forming a broad band laterally; few setae elsewhere; epipleurum and basal half of sternellum with dense, long, slender, projecting setae; sternum granulose, without setae. Mesothorax with posterior sixth of notum exceedingly finely granulose, with sparse row of setae near anterior margin, broadening into sparse band laterally; sternum, epipleurum and sternellum with long, fine, projecting setae. Metathorax similar to mesonotum, but without granulose posterior margin.

Abdominal segments one through seven similar, subquadrate in dorsal aspect; dorsum with sparse rows of very fine setae near anterior margin, most evident laterally near spiracle; posterior margin sometimes with few fine setae; spiracle elongate elliptical, of annular type, subtended by four setae; sternum with sparse band of fine setae along anterior margin, single seta on each side three-fourths distance to posterior border. Eighth abdominal segment similar, but with row of fine setae near posterior margin and cluster of setae posterolaterally. Ninth segment (Fig. 25) with tergum tapering to acutely rounded apex; dorsal surface densely set with short spines, mostly directed anterodorsad; sparsely set with longer, fine setae, also directed anterodorsad; urogomphi absent; lateral tergal margins densely set with long, fine setae; ventral margin of tergum with narrow band of short spines bordering concavity receiving tenth sternite (Fig. 19); tenth sternite with short spines laterally and on pygopods.

Prothoracic leg (Fig. 26) with dense clusters of nearly contiguous globular granules on mesal surfaces of trochanter and femur; posterior surfaces of trochanter, femur and tibia less densely set with granules; mesal apex of femur, mesal surface of tibia and base of claw bearing combs of stout spines; ectal surfaces of femur and tibia with brushes of long, slender setae. Meso- and metathoracic legs (Fig. 27) mesally with irregular combs of spines, ectally with longer, slender setae; claws without setation.

First instar larva (Fig. 28).—Length 5.1 mm; head capsule width 0.75 mm. Pale creamy white except for tan urogomphi, egg bursters, tips of claws and mandibles, and clavate setae on labrum and mandibular base. Six specimens, one pharate with setation of second instar visible through cuticle.

Cranium finely rugulose with few slender setae. Mandibles each with single large articulated fusiform spine near base of lateral margin (Fig. 29). Labrum with similar paramedial spines. Prothorax rugulose with sparse transverse row of about five extremely fine, pale setae back from anterior margin (Fig. 29); similar sparse row near posterior margin; egg bursters absent. Mesothorax and metathorax with few pale, extremely fine setae near posterior margin; short, spinose egg burster located laterodorsally on each side slightly behind middle, supertended closely by fine seta. Ab-

dominal segments one through eight similar, slightly larger than metathorax; each segment with few extremely fine, pale setae and egg burster located as on metathorax. Ninth abdominal segment parabolic in dorsal aspect, with pair of subcontiguous, strongly divergent, short and sharply pointed urogomphi at apex; dorsal surface with few extremely fine, pale setae; pygopods short, fleshy, without spination; spiracles circular. Prothoracic leg (Fig. 30) with three stout, blunt, clavate pigmented spines on mesal surface of trochanter; two on femur and single sharp spine on tibia, subtending claw; ectal surfaces with few extremely fine setae. Mesothoracic and metathoracic legs with few fine setae.

In addition 16 specimens of various intermediate instars (second onwards) were examined. These are similar to late instar specimens, but have fewer granules on the cranium, legs and ninth abdominal tergum, as described by Brown (1973) for *Philolithus.*

Egg.—Elongate ovoid as described by Brown (1973); length 3.7 mm, width 1.1 mm. Chorion very finely, shallowly rugulose.

The larvae examined were laboratory-reared from two collections of adults: California, Imperial County, Mountain Springs, 2,300′, III-27-1979, K. W. Brown. Mexico, Baja California Norte, Arroyo Catavina, IV-2-1976. J. T. Doyen and P. A. Rude [J. Doyen Lot No. 76D1.1].

Microschatia cedrosensis, new species
(Fig. 31)

Black beetles with coarsely, confluently punctate pronotum and strongly costate elytra.

Holotype male.—Frons set with coarse, setiferous punctures, nearly contiguous between eyes, becoming sparser, somewhat irregular anteriorly and then finer and subcontiguous around epistomal margin. Epistoma shallowly, arcuately emarginate anteriorly, scarcely indented at epistomal sutures. Labrum missing. Eye with barely noticeable prominence at apex of dorsal lobe; constriction almost half width of dorsal lobe. Antennal length about one and one-half times head width; segments four to nine distinctly longer than wide; ten trapezoidal, asymmetrical, slightly wider than long; eleven strongly asymmetrical; all segments set with moderately dense, coarse black setae, eleven with setae only on inner angle. Mentum broadly, shallowly emarginate with shallow median notch. Ligula missing. Postgenal process obtuse with very broadly rounded apex. Gular pedestal shallowly, arcuately emarginate.

Pronotum widest slightly before middle, about three-fourths as wide across anterior angles as basal; anterior angles acute with rounded apex; posterior angles nearly right angled, slightly exerted, not prolonged posteriorly; lateral margins scarcely explanate; posterior margin biconvex, with middle part almost twice width of lateral parts. Disk set with very coarse, deep, setiferous punctures, confluent laterally, becoming punctatorugose near margins and with irregular impunctate regions centrally; setae black, subspinose, decumbent. Hypomeron sparsely, coarsely punctate, more densely so near lateral carina. Prosternum tuberculopunctate anteriorly and laterally, becoming coarsely, confluently punctate on process. Prosternal process narrowly rounded.

Elytral base slightly wider than thoracic base; disk with sutural and four lateral polished, rounded costae; the two medial and the lateral-most costae reaching elytral

Fig. 31. *Microschatia cedrosensis* Brown and Doyen.

base; third costa ending at about level of metacoxae; intercostal spaces irregularly tuberculate or tuberculorugose, shagreened. Epipleural carina fine, distinct from humerus to elytral apex; epipleuron narrowing a little more abruptly near humerus, then gradually to apex. Legs as in *rockefelleri.*

Measurements.—Pronotal length 4.9 mm; greatest pronotal width 5.5 mm; elytral length 11.4 mm; greatest elytral width 7.7 mm.

Holotype male.—California Academy of Sciences, San Francisco.

Type locality.—Mexico, Baja California Sur, NE end Cedros Island, II-27-1952, J. P. Figg-Hoblyn.

Diagnosis.—*Microschatia cedrosensis* is similar to *costulata* Brown and Doyen but has the pronotal disk very coarsely, confluently punctate (much more finely, discretely punctate in *costulata*). In *cedrosensis* the elytral costae are all subequal in thickness and contour; in *costulata* the two medial costae are flattened and much thicker than the lateral two, which are acutely rounded.

Individuals of *M. championi* from coastal areas (San Quintin, Guerrero Negro) have coarsely punctate pronota, but have punctatorugose elytra without trace of costae.

Distribution and material examined.—Known only from the holotype.

Microschatia costulata, new species
(Fig. 32)

Brownish black or black beetles with discretely punctate pronotum and strongly costate elytra.

Female.—Frons and epistoma set with coarse, setiferous punctures, denser and finer on lateral epistomal margins and with few irregular impunctate areas on frons. Epistoma very shallowly (almost truncate) to shallowly emarginate, scarcely indented at lateral epistomal sutures. Eye with moderate prominence at apex of dorsal lobe; constriction about half width of dorsal lobe. Antennal length about one and one-third times head width; segments four to seven subquadrate, eight to ten wider than long; ten asymmetrical; eleven strongly asymmetrical; all segments set with moderately dense, coarse black setae, eleven with setae only on outer angle. Mentum broadly emarginate with median notch very shallow. Ligula almost twice as broad as notch, exposed. Postgenal process very obtuse with very broadly rounded apex. Gular pedestal shallowly, arcuately emarginate.

Pronotum widest at middle; about three-fourths as wide across anterior angles as basal; anterior angles acute with briefly rounded apex; posterior angles obtuse, neither exerted nor produced posterad; lateral margins thick, narrowly explanate; posterior margin biconvex with middle part almost twice width of lateral parts. Disk set with punctures as on frons, becoming rugulose on explanate part of lateral margins. Hypomeron and prosternum as in *cedrosensis.*

Elytral base slightly wider than or subequal to thoracic base; disk with sutural and four lateral costae; sutural and next two costae very broad, flattened, smooth and polished; two lateral costae narrow, subcarinate, crenulate; two medial intercostal spaces punctatorugose, sometimes with a few tubercles; three lateral interspaces tuberculorugose and with few anastomosing cross-carinae. Epipleural carina fine, continuous from humerus to elytral apex, but irregularly crenulate, interrupted; epipleuron narrowing a little more abruptly near humerus, then gradually to apex. Legs as in *rockefelleri.*

Male.—Differs as indicated in generic description.

Measurements.—Pronotal length 4.1 to 4.9 mm; greatest pronotal width 5.6 to 7.1 mm; elytral length 9.1 to 12.2 mm; greatest elytral width 6.1 to 8.3 mm.

Fig. 32. *Microschatia costalata* Brown and Doyen.

Holotype female (United States National Museum).—California, San Diego, Coll. Chittenden. One male and one female paratype from Mexico, Baja California Norte, San Quintin, V-9-1938, H. A. Brandt. The holotype and both paratypes appear to have been collected dead. The holotype (figured) is missing some tarsomeres and the apical two segments of each antenna and bears a hole in the left elytron and one in the base of the abdomen. These specimens are dark reddish black.

Diagnosis.—*Microschatia costulata* and *M. cedrosensis* appear to be sister species. The characters which differentiate them are detailed under the latter.

Distribution.—San Diego, California south to Bahia de San Quintin, Baja California Norte. Nothing is known of the habitat of this rare species. Most collection localities are coastal.

Additional material examined.—Baja California Norte, San Quintin, V-9-1938 (1 fragment); Santa Ynez, V-1983 (1).

Microschatia inaequalis LeConte
(Fig. 33)

Microschatia inaequalis LeConte, 1851:129.
Microschatia puncticollis LeConte, 1851:129.
Pycnonotida inaequalis Casey, 1912:92.
Pycnonotida puncticollis Casey, 1912:93.
Pycnonotida laxicollis Casey, 1912:91. NEW SYNONYMY.
Pycnonotida diversa Casey, 1912:92. NEW SYNONYMY.
Pycnonotida araneoides Casey, 1912:92. NEW SYNONYMY.
Pycnonotida impar Casey, 1912:92. NEW SYNONYMY.

Black or blackish brown beetles, occasionally with narrow, bluish white body margins; pronotum punctatorugose or tuberculorugose; elytra very coarsely rugose.

Female.—Frons and epistoma punctatorugose; depressions with sparse, coarse, brownish-black, decumbent setae. Epistoma moderately, arcuately emarginate anteriorly, scarcely indented at epistomal sutures. Eye with slighest prominence anterad of apex of dorsal lobe; constriction about half width of dorsal lobe.

Antennal length about one and one-third times head width; segments four to seven longer than broad; eight to ten trapezoidal, noticeably asymmetrical; eight subquadrate, nine and ten wider than long; eleven strongly asymmetrical; all segments set with moderately dense, coarse, black setae, eleven with setae only on inner angle. Mentum broadly, shallowly emarginate with very shallow median notch. Ligula about one and one-half times broader than notch, very small but exposed. Postgenal process obtuse; apex rounded to broadly rounded. Gular pedestal slightly emarginate.

Pronotum widest at about middle, about three-fourths as wide across anterior angles as basal; anterior angles acute to nearly right angled, with rounded apex; posterior angles strongly obtuse, very narrowly rounded, neither exerted or produced posterad; lateral margins crenulate, narrowly to moderately explanate, reflexed upward near basal corners, sometimes with narrow zone of faint, bluish white, flocculent material (probably wax); posterior margin biangulate with middle part about one and one-half times width of lateral parts. Disk finely tuberculorugose anteriorly, usually becoming punctatorugose posteriorly and along lateral margins; depressions set with short, decumbent setae; hypomeron tuberculopunctate or tuberculorugose; prosternum much more coarsely tuberculopunctate, becoming punctatorugose on process. Prosternal process broadly rounded.

Elytral base wider than or occasionally subequal to thoracic base, with humeral margin of epipleuron raised, forming distinct vertical ridge; disk very coarsely, irregularly rugose, often with overlay of fine tubercles, especially laterally; rugae sometimes tending to form one or more very convoluted, irregular longitudinal ridges; sutural area usually relatively smoother than remainder of elytra; lateral margin just above epipleural carina sometimes with narrow zone of faint, bluish white, flocculent material (probably wax). Epipleural carina crenulate, interrupted by rugae, but distinct from humerus to elytral apex; epipleuron punctatorugulose anteriorly, becoming rugulose posteriorly; gradually narrowing from base to apex. Abdominal sternites densely set with moderately coarse, setiferous punctures to asperately punctatorugose. Femora densely, asperately punctate to finely tuberculopunctate; setae coarse, black, declined. Middle and hind tibia asperately or tuberculosetose; setae finely to mod-

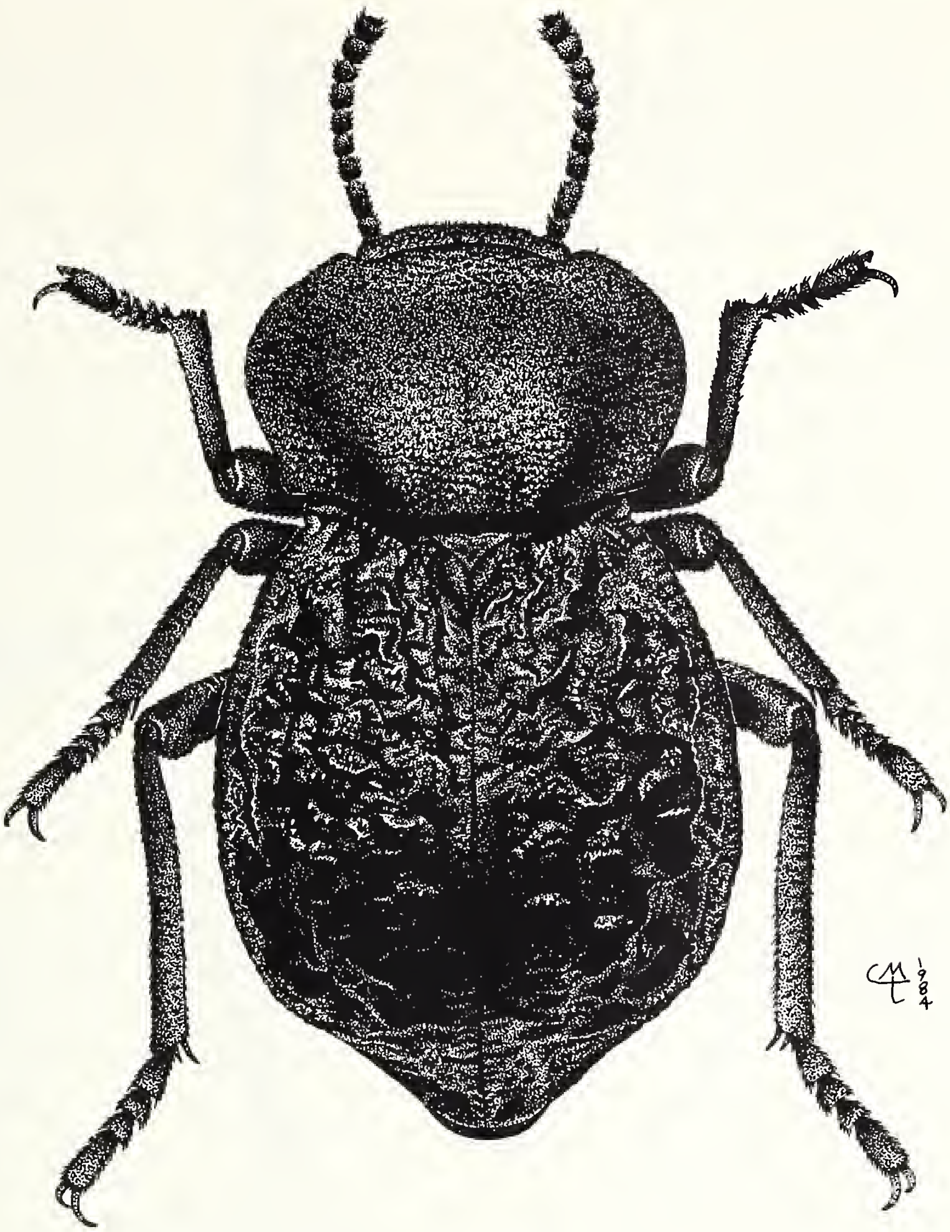


Fig. 33. *Microschatia inaequalis* LeConte.

erately coarsely spinose; anterior tibia tuberculosetose with coarse, blunt spines ventrally, finer sharp spinose setae dorsally.

Male.—Differs as indicated in generic description.

Measurements.—Pronotal length 3.5 to 5.4 mm; greatest pronotal width 5.3 to 8.1 mm; elytral length 7.2 to 12.6 mm; greatest elytral width 5.5 to 8.9 mm.

Holotype (sex not determined).—Museum of Comparative Zoology, Harvard University.

Type localities.—Of *inaequalis,* San Diego; of *puncticollis,* "Warners" [Warner Springs]; of *diversa,* "vicinity of San Diego" (all San Diego County, California); of *laxicollis, araneoides,* and *impar,* southern California.

Diagnosis.—The tuberculopunctate pronotal disk and tuberculate hypomeron distinguish *M. inaequalis* from all other *Microschatia.* It is most similar to very coarsely sculpted individuals of *championi*; in those specimens, however, the pronotal disk is coarsely, closely punctate or punctatorugose and the hypomeron is coarsely punctate, never tuberculate. In addition, the elytral rugosity of *inaequalis* is almost always

overlain by fine tubercles. In *championi* tubercles are never present. *Microschatia polita* Horn is similar to *inaequalis* in body shape, but it is easily distinguished by its smooth, highly polished integument (coarsely punctate, punctatorugose or tuberculorugose and usually dull in *inaequalis*).

Variation.—Two individuals labeled Anza Borrego Desert have the pronotal disk coarsely, confluently punctate, with only faint indications of tubercles near the anterior margin. The elytra of these specimens are much less rugose than typically, and are somewhat polished and shining, without setae and with only a few very fine tubercles anterolaterally. These correspond to *puncticollis* LeConte. However, two specimens from Borrego Springs have the pronotal disk tuberculopunctate and the elytra strongly rugose, dull and overlain by tubercles, as usual. A few individuals have the dorsal setae reddish brown rather than black, but do not differ otherwise. The bluish white (wax ?) deposits on the lateral margins of the elytra and occasionally the pronotum range from very evident to extremely faint, and are absent from many individuals. None of the features described above shows any obvious geographic patterning. All the species described by Casey (1912) clearly lie within the normal range of variation of *inaequalis,* and are here placed in synonymy without further explanation.

Distribution.—Northern Baja California Norte and California south of the Los Angeles Basin, in a variety of arid and semiarid habitats including coastal scrub, sparse savannah woodland, chaparral, and Sonoran Desert.

Material examined.—California. Los Angeles County, La Mirada, I-7-1976 (1); Los Angeles, IV-9-1955 (1); (no date) (1). Orange County, Costa Mesa, VII-11-1957 (1); Fullerton, IV-30-1952 (1); Laguna Beach, III-31-1962 (1); IV-15-1949 (1); VI-27-1932 (1); Newport Beach, IV-28-1962 (17); Sand Canyon, II-26-1972 (1); lower Trabuco Canyon, IV-7-1962 (1). Riverside County, Box Springs Mountains, II-9-1964 (1); III-1-1965 (1); IV-18-1964 (3); Box Springs Canyon, III-1964 (1); Gavilan Hills, II-20-1965 (1); the Gavilan, IV-18-1937 (1); Grand Terrace, IV-12-1964 (3); Riverside, I-10 to VII-21 (various years) (29). San Bernardino County, Victorville, IV-14-1962 (1). San Diego County, Alvarado, V-19-1949 (1); Anza Borrego Desert, III-22-1978 (2); Borrego Springs, IV-15-1978 (1); Daylight, II-22-1956 (1); Flinn Springs County Park, IV-28-1962 (1); Lakeside [15 mi E San Diego], XII-22-1910 (1); (no date) (1). La Jolla, IV-28-1969 (5); XII-20-1910 (2); La Mesa, III-2-1958 (1); III-23-1951 (1); Mission Valley, II-8-1934 (1); II-22-1934 (1); Otay, V-18-1943 (1); Ramona, III-7-1942 (1); San Diego, I-25/26-1888 (13); I-1909 (1); II-2-1899 (1); II-10-1988 (1); III-1899 (1); IV-21-1921 (1); I-26 (1); III-2 (1); III-10 (24); VIII-13 (1); (no date) (24). Mexico. Baja California Norte, Cantamar, 5 km S, X-22-1981 (1); Ensenada, I-5-1925 (1); IV-17-1973 (1); (no date) (11); Punta Banda, II-23-1935 (2); Rosarito Beach, XI-12-1956 (2); 7.5 mi S Santo Tomas (2); 10 mi N San Vicente, III-25-1973 (1); Todos Santos Island, V-25-1923 (1).

Microschatia polita Horn
(Fig. 34)

Microschatia polita Horn, 1893:141.
Pycnonotida polita, Casey, 1912:93.

Polished, shiny black beetle with finely punctate dorsum.

Holotype female.—Frons and epistoma finely shagreened, sparsely, shallowly punc-

Fig. 34. *Microschatia polita* Horn.

tate. Epistoma very shallowly emarginate anteriorly, scarcely indented at epistomal sutures. Eye partly concealed by pronotum, but constriction apparently about half width of dorsal lobe. Antenna about one and one-fourth times head width; segments four to seven longer than wide, eight subquadrate, nine and ten wider than long; eleven strongly asymmetrical; setation as in *inaequalis.* Mentum very shallowly emarginate with shallow median notch. Ligula almost twice as broad as notch, bidentate. Postgenal process obtuse, apex broadly rounded. Gular pedestal moderately emarginate.

Pronotum widest at about middle, about four-fifths as wide across anterior angles as basal; anterior angles acute with rounded apex; posterior angles obtuse, neither produced nor exerted; lateral margins narrowly explanate, crenulate; posterior margin biangulate with middle part about one and three-fourths times as wide as lateral parts. Disk set with very fine, sparse, minutely setigerous punctures; polished, shining centrally, shagreened near anterior margin, shagreened and rugulose near lateral margins. Hypomeron punctate; prosternum tuberculopunctate, becoming punctatorugose on process; process narrowly rounded.

Elytral base slightly wider than thoracic base with humeral margin of epipleuron

minutely everted; disk smooth with weak undulations; wrinkled along suture; shiny, with fine sparse setigerous punctures centrally, becoming finely, sparsely tuberculate laterally. Epipleural carina sharp, distinct from humerus to apex. Epipleuron narrowing slightly more rapidly to hind coxa then gradually to elytral apex. Abdominal sternites shagreened with fine, sparse setigerous punctures. Legs as in *inaequalis.*

Measurements.—Pronotal length 4.2 mm; greatest pronotal width 5.9 mm; elytral length 10.7 mm; greatest elytral width 6.9 mm.

Holotype female.—Museum of Comparative Zoology, Harvard University.

Type locality.—Arizona.

Diagnosis.—Similar in body shape to *M. inaequalis*; *M. polita* is easily distinguished by its smooth, shiny, finely punctate dorsum.

Distribution.—Known only from the holotype.

Microschatia planata Doyen and Brown, new species
(Fig. 35)

Weakly shining, black beetles with broadly explanate pronotum and smooth, finely punctate elytra. Tibia of fore and middle legs flattened, laterally carinate.

Female.—Frons and epistoma with fine, subcontiguous, minutely setigerous punctures, closer laterally, with small, irregular impunctate areas medially. Epistoma very shallowly emarginate, almost truncate; scarcely indented at lateral sutures. Labrum very shallowly emarginate or subtruncate anteriorly. Eye moderately narrow, with small but distinct prominence at apex of dorsal lobe; consriction about two-thirds width of dorsal lobe. Antennal length about one and one-fifth times head width; segments four to seven longer than broad; eight subquadrate; nine and ten asymmetrical, wider than long; segments two to ten set with moderately dense, coarse, black setae; eleven with apical margin ringed with setae, longest on inner angle. Mentum broadly, moderately deeply emarginate with moderate median notch. Ligula about one and one-half times as broad as notch, exposed. Postgenal process slightly obtuse, broadly rounded. Gular pedestal shallowly emarginate.

Pronotum widest at about middle, about four-fifths as wide across anterior angles as basal; anterior angles obtuse, broadly rounded; posterior angles nearly right angled, neither produced nor exerted; lateral margins somewhat thickened, strongly explanate; posterior margin biangulate, with middle part about three times as wide as lateral parts. Disk with moderate paramedian gibbosities and very shallow, broad medial depression in posterior sixth; central area set with minutely setigerous punctures slightly larger than those on head, becoming coarser laterally and then deeply, reticulately punctate on explanate part of margins; becoming finer, sparser posteromedially. Hypomeron smooth except rugulose near lateral carina; sometimes with few fine, deep punctures near prosternum. Prosternum deeply tuberculopunctate, becoming reticulately punctate on process. Prosternal process slightly declivous behind coxa, with acutely rounded or subsaggitate apex.

Elytral base slightly narrower than thoracic base, humeral margin of epipleuron weakly raised; anterior margin with small gibbosities opposing those on pronotum; disk slightly undulating, smooth, weakly shining, with sparse punctures slightly smaller to slightly larger than those on pronotum; becoming more coarsely punctate or punctatorugose laterally. Epipleural carina fine, distinct from humerus to elytral apex;

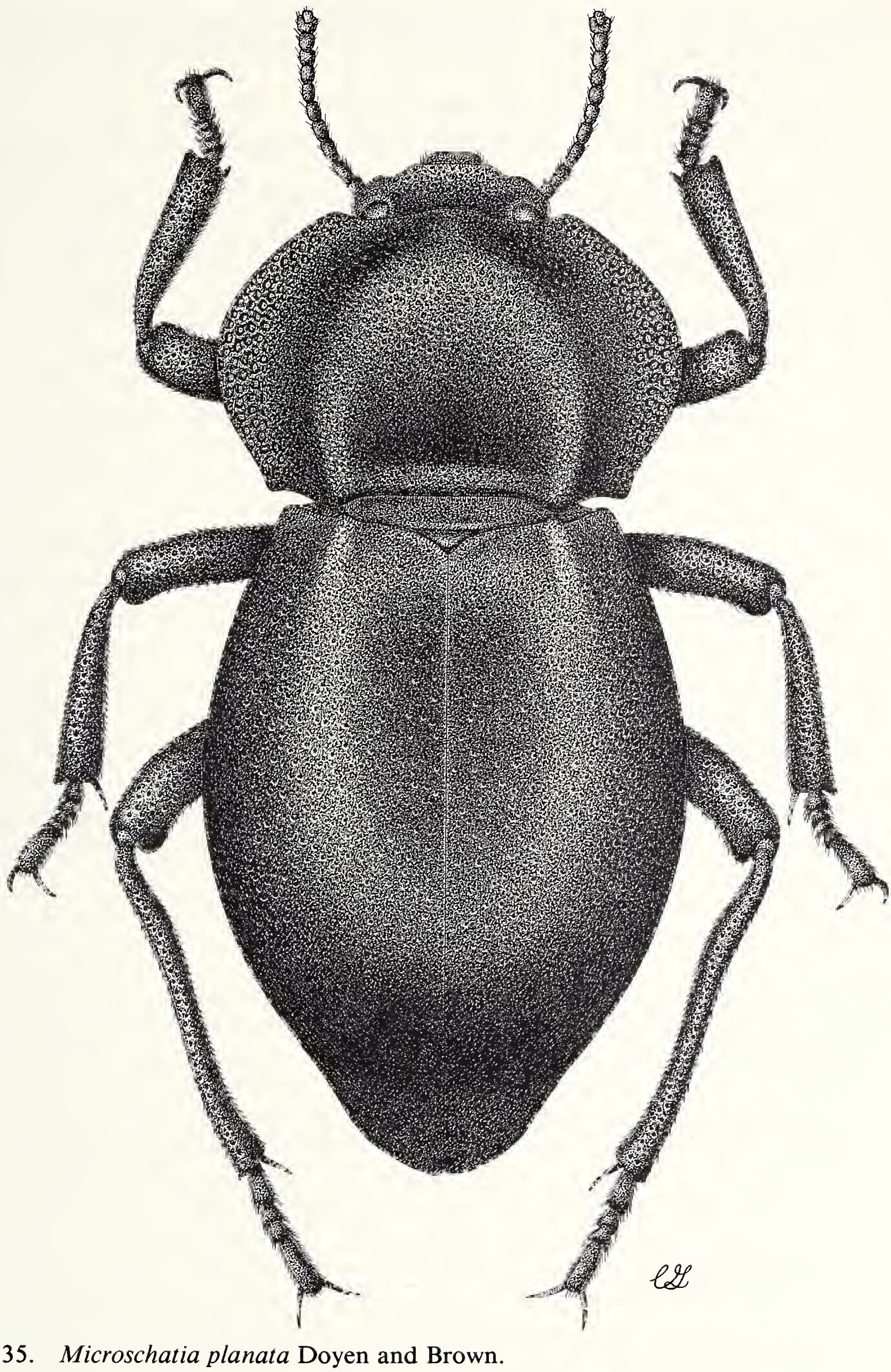


Fig. 35. *Microschatia planata* Doyen and Brown.

epipleuron sculpted like disk, narrowing more rapidly to metacoxa, then gradually to elytral apex. Abdominal sternites smooth, shining; surface finely punctate on first four, more coarsely so on fifth; sternites three and four with irregular impunctate medial areas. Femora densely, sometimes subcontiguously set with deep, setigerous

punctures; setae short, black. Anterior and middle tibiae flattened with subcarinate outer magin; anterior tibia with anterior spur much larger than posterior. Posterior tibia weakly to moderately arcuate.

Male.—Differs as indicated in generic description.

Measurements.—Pronotal length 5.9 to 7.6 mm; greatest pronotal width 8.8 to 11.7 mm; elytral length 8.0 to 12.1 mm; greatest elytral width 9.2 to 12.0 mm.

Holotype female [CAS] and 88 paratypes from Mexico, Baja California Norte, Miller's Landing, IV-6-1976, J. Doyen, on sand dunes at night; 21 paratypes, same locality, III-29-1973. Miller's Landing is approximately 50 km ESE of Punta Prieta; 23 paratypes, Baja California Sur, 9 km N Guerrero Negro, sand dunes, IX-8-1977, E. Fisher, R. Westcott; 15 paratypes same locality, III-23/24-1987, J. Doyen, S. Stockwell.

Diagnosis.—Its flattened fore and middle tibiae and curved hind tibia distinguish *planata* from all other *Microschatia* (tibiae round; straight in others). The broad, explanate pronotum and overall flattened appearance are also distinctive. This is the largest species of *Microschatia.*

Distribution and habitat.—Endemic to the Vizcaino region of Baja California, where it inhabits sandy substrates, especially aeolian sand dunes. The beetles occur in very large numbers in some years. They are diurnally active in cool, overcast situations, otherwise, nocturnal. The modifications of the legs appear to be adaptations for digging into the sand, in which the beetles shelter during most days.

Additional material examined.—Mexico, Baja California Norte, 1.8 km SE Miller's Landing, VI-27/28-1973 (2). Baja California Sur, Guerrero Negro, 2 mi N, VI-25/26-1977 (2); 5 km N, VIII-25-1975 (2); 9 mi N, III-23/24-87 (12); 11.3 km N, IV-10/11-1976 (12); 15 mi N, III-23-87 (2); 9 km N, IX-8-77 (5); 7 mi W, IV-7-1976 (1); 7 mi SE, IV-8-1976 (1); 24 km SE, IV-11-1976 (1); 47 km SE, I-15/16-1974 (1); 66 rd km W Vizcaino, III-24/25-1980 (2).

ACKNOWLEDGMENTS

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Appendix 1. Character list. Primitive character states are coded a; derived states, b. For discussion see text.

0. Labrum shape—anterior border (Fig. 1)
    a. Shallowly emarginate (0)
    b. Deeply emarginate (1)
1. Lateral epistomal margin (Fig. 2)
    a. Straight or weakly indented (0)
    b. Deeply, angulately indented (1)
2. Anterior epistomal margin (Fig. 2)
    a. Shallowly concave (0)
    b. Deeply concave (1)
3. Eye shape (Fig. 3)
    a. Very narrow, strongly constricted by epistomal canthus (0)
    b. Moderately narrow, weakly constricted (1)
4. Mentum, anterior margin (Fig. 4)
    a. Shallowly, broadly notched (0)
    b. Deeply, narrowly notched (1)
5. Ligula (Fig. 4)
    a. Exposed, relatively large (0)
    b. Concealed, relatively small (1)
6. Antennal length
    a. Short, less than 1.1 (female) or 1.45 (male) width of head (0)
    b. Longer, more than 1.2 (female) or 1.5 (male) width of head (1)
7. Antennal segment 10, shape (Fig. 5)
    a. Subquadrate (0)
    b. Wider than long (1)
8. Antennal segment 10, sensory tomentum (Fig. 5)
    a. Tomentose sensory patches subequal (0)
    b. Outer patch much larger than inner (1)
9. Pronotum, shape of disk (Fig. 6)
    a. Much narrower at base than at widest point (0)
    b. Slightly narrower at base or subequal to widest point (1)
10. Pronotum, posterior corners (Fig. 6)
    a. Obtuse or right angled (0)
    b. Acute (1)
11. Pronotum, posterior border (Fig. 6)
    a. Arcuate (0)
    b. Bisinuate or biangulate (1)
12. Pronotum, posterior gibbae
    a. Very weak or absent (0)
    b. Strong (1)
13. Relative width of elytral base (Fig. 6)
    a. Equal to or wider than base of thorax (0)
    b. Narrower than base of thorax (1)
14. Hypomeron, sculpture
    a. Smooth (0)
    b. Punctate or tuberculate (1)
15. Prosternal process, shape (Fig. 7)
    a. Broadly rounded or truncate (0)
    b. Narrowly rounded to sagittate (1)

Appendix 1. Continued.

16. Elytral shape (Fig. 6)
    a. Much narrower at base than at widest point (0)
    b. Slightly narrower at base (1)
17. Elytral sculpture (I)
    a. Smooth, punctate (0) (Figs. 12, 18)
    b. Rugose or reticulate (1) (Figs. 13, 14, 15, 21)
18. Elytral sculpture (II)
    a. Non-costate (0) (Figs. 12, 13, 18, 22, 23)
    b. Costate (1) (Figs. 14, 16, 17, 19, 20)
19. Elytra, humeral angle (Fig. 8)
    a. Strong, projecting forward (0)
    b. Weak, not projecting forward (1)
20. Epipleuron, basal width (Fig. 8)
    a. Moderately wide (0)
    b. Very wide (1)
21. Epipleuron, shape (Fig. 8)
    a. Narrowed evenly from humerus to elytral apex (0)
    b. Narrowed more rapidly near humerus, then evenly to apex (1)
22. Epipleural carina (Fig. 8)
    a. Distinct from humerus to elytral apex (0)
    b. Obsolete or absent in posterior half (1)
23. Body surface
    a. Clean (0)
    b. With earthen coating in certain regions (1)
24. Body setation
    a. All setae simple, hairlike (0)
    b. Some setae flattened, scale-like (1)
25. Thoracic/elytral setation
    a. Margined by dense scaling (0)
    b. Setae sparsely, evenly distributed (1)
26. Setation on legs
    a. Black (0)
    b. Whitish or yellowish (1)
27. Tarsomere configuration
    a. Slender (0)
    b. Thickened (1)
28. Antennal segment thickness
    a. Slender (0)
    b. Thickened, ± moniliform (1)
29. Mentum size (Fig. 4)
    a. Smaller than buccal opening; not contacting postgenae (0)
    b. Filling buccal opening; contacting postgenae except at corners (1)
30. Prosternal process shape
    a. Declivous (0)
    b. Porrect (1)
31. Configuration of antennal apex
    a. Segment 11 about half as large as 10; segment 10 not emarginate (0)
    b. Segment 11 about one-fourth size of 10; 10 deeply emarginate (1)

Appendix 2. Character × OTU Matrix. Character states are defined in Appendix 1 and discussed in text. States in parentheses occur occasionally and were not used in computations.

Character	*punctata*	*solieri*	*robusta*	*sulci-pennis*	*rocke-felleri*	*morata*	*cham-pioni*	*cedro-sensis*	*costulata*	*polita*	*inae-qualis*	*planata*
0	1	1	1	1	1	1	0	0	0	0	0	0
1	1	1	1	1	1	1	0	0	0	0	0	0
2	1	1	1	0	0	0	0	0	0	0	0	0
3	1	1	1	1	1	1 (0)	0 (1)	0	0	0	0	0
4	1	1	1	0	0	0	0	1 (0)	0	0	1	1
5	1	1	1	0	0	0	0	0	0	0	0	0
6	1	1	1	0	0	0	0	0	0	0	0	1
7	1	1	1	0	0	0	1	1	1	1	1	1
8	0	0	0	0	0	0	1	1	1	1	1	1
9	0	0	1	1	1	1	0	0	0	0	0	0
10	0	0	1	1	1	1	0	0	0	0	0	0
11	1	1	0	0	0	0	1	1	1	1	1	1
12	0	0	0	0	0	0	1	1	1	1	1	1
13	1	1	0	0	0	0	1 (0)	1	1 (0)	0	1 (0)	1
14	0	0	0	1	1	1	0	1	1	0	1	0
15	0	0	0	0	0	0	1	1	1	0	1	1
16	0	0	1	1	1	1	0	0	0	0	0	0
17	0	1	1	1	1	1	0 (1)	1	1	0	1	0
18	0	0	1	1	0	1	0	1	1	0	0 (1)	0
19	1	1	1	1	1	1	0	0	0	0	0	0
20	0	0	0	1	1	1	0	0	0	0	0	0
21	1	1	1	0	0	0	1	1	1	1	0	1
22	1	1	1	0	0	0	0	0	0	0	0	0
23	1	1	1	0	0 (1)	0 (1)	0	0	0	0	0	0
24	1	1	1	1	1	1	0	0	0	0	0	0
25	0	0	0	1	1	1	0	0	0	0	0	0
26	1	1	1	0	0	0	0	0	0	0	0	0
27	1	1	1	1	1	1	1	1	1	1	1	1
28	1	1	1	1	1	1	1	1	1	1	1	1
29	1	1	1	1	1	1	1	1	1	1	1	1
30	1	1	1	1	1	1	1	1	1	1	1	1
31	1	1	1	1	1	1	1	1	1	1	1	1

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RHYSSOCEPHALA, NEW GENUS, WITH THE DESCRIPTION OF THREE NEW SPECIES (HETEROPTERA: PENTATOMIDAE)[1]

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Abstract.—The pentatomid genus *Arocera* Spinola *sensu lato* is divided into two genera, one of which, *Rhyssocephala,* is described as new. *Arocera colombiana* McDonald, *A. inmaculata* (Pirán), *A. principalis* (Stål), *A. rufolimbata* Stål, *A. rufonotata* Stål, *A. splendens* (Blanchard), and *A. verdana* McDonald are all transferred to *Rhyssocephala.* Diagnoses are provided for all previously described species. Three new species are described: *R. ecuadoriensis* from Ecuador, *R. mcdonaldi* from Panama and northwestern South America, and *R. infuscata* from Mexico and Central America. *Arocera colombiana* McDonald, 1984, is placed as a junior synonym of *Pentatoma principalis* Stål, 1855. A lectotype designation is made for *A. rufonotata* Stål, 1861. A key to the genera that include species similar in color to *Arocera* and *Rhyssocephala* is given, as well as a key to species of *Rhyssocephala.*

In his revision of the genus *Arocera* Spinola, McDonald (1984) indicated that the species could be separated into two groups based on the shape of the male parameres. He further noted that females of the species would also form two distinct groups according to the shape of the eighth paratergites and the spermathecal bulb. He did not, however, emphasize that the groups defined by the male specimens were identical to the groups defined by the female specimens.

Several other characters (male pygophore, female spermatheca, dorsal coloration, texture of the dorsal surface of the head) also separate the known *Arocera* species into the same "species groups." I believe these two groups are so consistently and distinctly different that each should be recognized as a genus. Because the type species of all available junior synonyms of *Arocera* belong to just one of the groups, a new genus must be erected for the remaining group of species. *Rhyssocephala,* new genus, is herein described.

Rhyssocephala belongs in the nominate subfamily and tribe of the Pentatomidae, is restricted to the New World, and contains several of the most brightly colored species of western hemisphere Pentatomidae. It is characterized by the lack of a spine or tubercle at the base of the third (second visible) abdominal sternite and elongate ostiolar rugae, each extending more than two-thirds the distance from the mesial margin of the ostiole to the lateral metapleural margin. Rolston and McDonald (1984) provided a key to related western hemisphere genera occurring north of South America, and Rolston (1987) presented a key to those South American genera that have

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both elongate ostiolar rugae and an unarmed abdominal venter. *Rhyssocephala* will key to *Arocera* in both of the above keys.

Due to misidentifications by recent workers and the discovery of several undescribed species, both *Arocera* and *Rhyssocephala* need further study. The present work provides a study of the species of *Rhyssocephala*; *Arocera* will be revised in a future paper. Keys are provided to the genera that include species similar in color to *Rhyssocephala* and *Arocera,* and to all known species of *Rhyssocephala.* Measurements are in millimeters; measurements in parentheses are of the holotype. Measurements of the body were taken with the anterior and posterior margins of the scutellum in approximately the same plane of focus. Total length was measured slightly differently in each sex. In females, total length was simply the distance from the apex of the head to the posterior apex of the body excluding hemelytral membranes. In males, the pygophore may be distended by varying amounts, and total length was measured from the apex of the head to the posterior-most part of the last connexival segment. Total width was measured across the humeral angles, although in some cases the width across the abdomen was greater. Head length was measured from the apex of the head to an imaginary line drawn through the posterior margins of the ocelli. Head width was measured across the eyes. When label data are presented in the text, each letter in parentheses represents a separate label with (a) being closest to the specimen. Label data for holotype and paratype specimens are quoted exactly as appears on the label. Determination labels and collection labels were sometimes omitted from the label data citations for brevity. Acronyms are defined in the acknowledgments.

The following key separates those genera which are similar in appearance to *Arocera* and *Rhyssocephala.* These genera are not necessarily closely related, but all include some species that are brightly colored with orange, red, yellow, or metallic-green or blue. It should be noted that many asopine genera are also brightly colored; they will be separated as a group in the first couplet.

KEY TO BRIGHTLY-COLORED NEW WORLD PENTATOMINAE GENERA

1. Rostrum crassate; bucculae more or less converging and meeting posteriorly . . . Asopinae
– Rostrum incrassate; bucculae not meeting posteriorly 2
2(1). Scent gland orifices inconspicuous, ostiolar canals or rugae and attending evaporative areas absent . . . . *Murgantia* Stål
– Scent gland orifices distinct, usually attended by ostiolar canals or rugae and shagreened evaporative areas 3
3(2). Base of third (second visible) abdominal sternite armed with forward-projecting spine or tubercle 4
– Base of abdominal sternite three unarmed 7
4(3). Metasternum produced ventrad, at least posteriorly, with posterior margin in apposition to abdominal spine or tubercle 5
– Metasternum not produced ventrad, abdominal spine or tubercle free distally, not in apposition to posterior margin of metasternum 6
5(4). Rostrum not extending beyond mesocoxae . . . . *Brachystethus* Laporte
– Rostrum extending onto base of abdomen . . . . *Pharypia* Stål
6(4). Distal end of first antennal segment exceeding apex of head . . . . *Vulsirea* Spinola
– Distal end of first antennal segment not surpassing apex of head . . . . . . *Roferta* Rolston

7(3). Ostiolar rugae extending less than one-half distance from mesial margin of ostiole to lateral metapleural margin 8
– Ostiolar rugae extending at least three-fourths distance from mesial margin of ostiole to lateral metapleural margin 9
8(7). Anterolateral margins of pronotum distinctly reflexed; antennae four-segmented .... *Boea* Walker
– Anterolateral margins of pronotum not reflexed; antennae five-segmented .... *Runibea* Stål
9(7). Dorsal surface usually yellow, orange, or red with brown or black markings; if dorsal surface mostly black then pronotum completely black; vertex of head nearly glabrous, impunctate; each paramere with basal process either obtuse or large and spatulate, not digitiform; caudal margin of proctiger entire, without posterior projections (Figs. 13, 14); ninth paratergites flat or only slightly concave (Figs. 19–21); spermathecal bulb globose, either constricted near base (Figs. 2, 4) or with digitiform process (Figs. 6, 12); dilation of spermatheca lacking sclerotized area near proximal end of sclerotized rod (Figs. 1, 3, 5, 11) .... *Arocera* Spinola
– Dorsal surface dark brown, black or metallic blue or green, with some yellow, orange, or red on anterior pronotal angles; vertex of head roughened, punctate, or rugulose; each paramere with basal process digitiform; caudal margin of proctiger with two projections, either projecting dorsad (Figs. 15, 16) or caudad (Figs. 17, 18); ninth paratergites distinctly bent near middle, inflated apically (Figs. 22–24); spermathecal bulb globose, lacking digitiform process (Figs. 8, 10); dilation of spermathecal duct with slightly sclerotized area near proximal end of sclerotized rod (Figs. 7, 9) .... *Rhyssocephala,* new genus

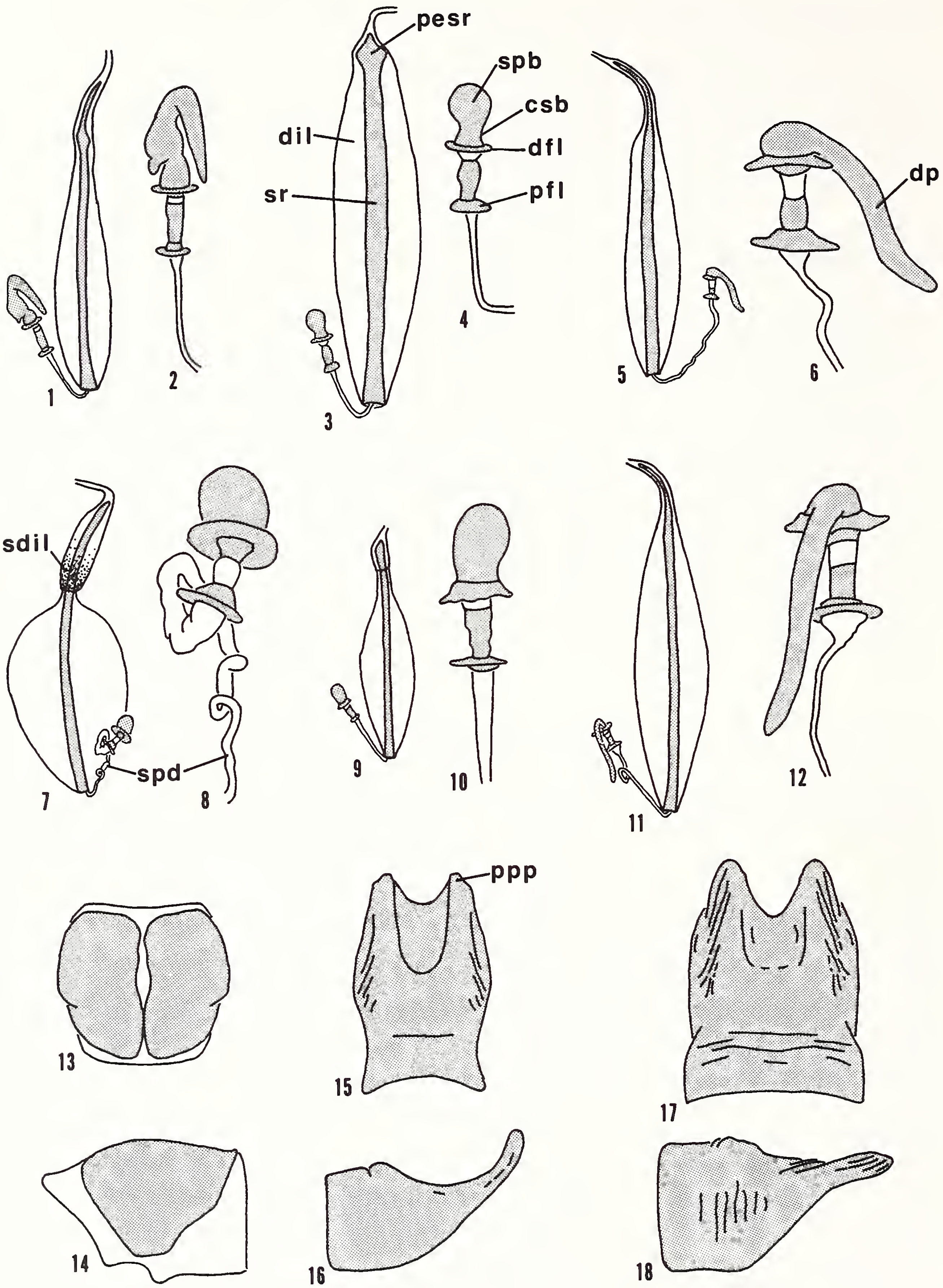
Rhyssocephala, new genus

Type species. *Arocera rufonotata* Stål, 1861.

Description. Dorsal coloration black, dark brown, or metallic green or blue with yellow, orange, or red markings; dorsal punctation usually minute, dense, often forming rugulose lines on scutellum.

Vertex of head roughened, punctate, or rugulose; jugal surfaces distinctly, diagonally wrinkled; lateral jugal margins sinuous, usually at least slightly reflexed, apices often slightly inflated; juga and tylus subequal in length. First antennal segment not surpassing apex of head. First rostral segment reaching at most only slightly beyond posterior margins of bucculae; posterior margins of bucculae not lobed; rostrum reaching to or beyond metacoxae. Anterolateral margins of pronotum straight to convex, distinctly reflexed. Ostiolar rugae elongate, reaching at least two-thirds of distance from ostiole to lateral metapleural margin. Tarsi three-segmented. Base of abdomen unarmed ventrally.

Each paramere Γ-shaped with small digitiform process near base. Posterior margin of proctiger produced caudally into two narrowly rounded projections (Figs. 15, 17). Inferior ridge of pygophore forming vertical wall, usually with few to many black spicules; dorsolateral angles produced dorsad and cephalad into black spiculate horns; ventral margin produced caudad, sometimes with mesial emargination. Ninth paratergites distinctly bent near middle, apices inflated (Figs. 22–24). Spermatheca with sclerotized rod not swollen near proximal end, not acuminate as in *Arocera* (Figs. 7, 9); dilation of spermatheca with slightly sclerotized portion near proximal end of



Figs. 1–18. 1, 2. *Arocera* (*A.*) *acroleuca.* 1. Spermatheca. 2. Spermathecal pump. 3, 4. *A.* (*A.*) *aequinoxialis.* 3. Spermatheca. 4. Spermathecal pump. 5, 6. *A.* (*Euopta*) sp. 5. Spermatheca. 6. Spermathecal pump. 7, 8. *Rhyssocephala splendens.* 7. Spermatheca. 8. Spermathecal pump. 9, 10. *R. infuscata.* 9. Spermatheca. 10. Spermathecal pump. 11–14. *A.* (*E.*) *spectabilis.* 11. Spermatheca. 12. Spermathecal pump. 13. Proctiger, dorsal view. 14. Proctiger, lateral view.

sclerotized rod (Figs. 7, 9); spermathecal bulb globose, lacking digitiform process, not constricted near base (Figs. 8, 10).

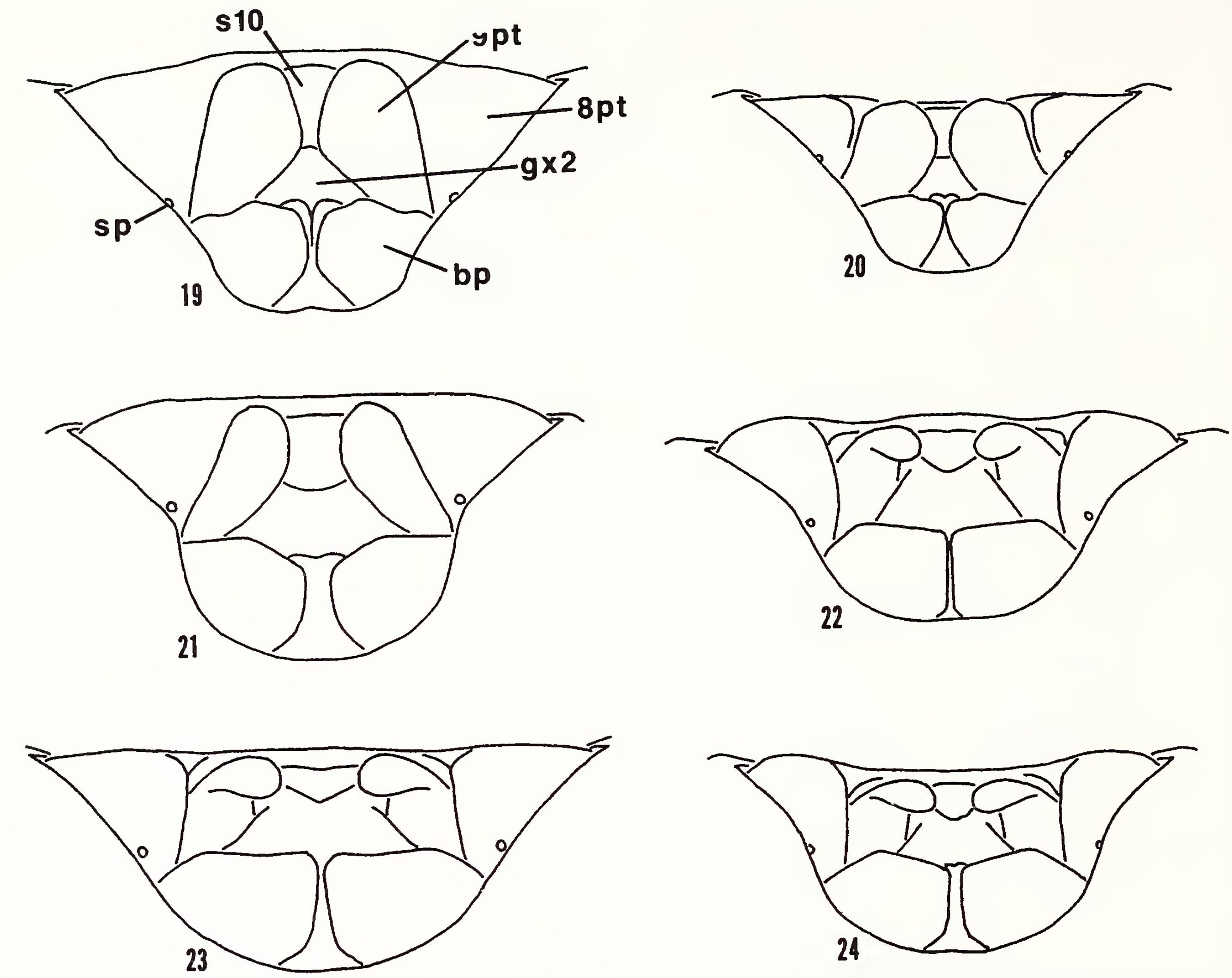
Comments. This genus contains nine species, all of which are black or metallic green or blue. The texture of the head and the density of the dorsal punctation will usually separate these species from *Arocera*. The structure of the male and female genitalia are also diagnostic.

KEY TO SPECIES OF RHYSSOCEPHALA, NEW GENUS

1. Dorsal surface brown with pronotum, scutellum, and coria contrastingly margined with black or metallic green (Fig. 25) (Colombia, Venezuela, Mexico?) .... *principalis* (Stål) (in part)
– Dorsal surface dark brown, black, or metallic green or blue, unicolorous except for some yellow or red markings 2
2(1). Dorsal surface metallic green with small, red spot on median of pronotum, usually with red spot in each basal angle of scutellum, and another triangular red spot on each corium near apex of scutellum (Fig. 32); anterolateral margins of pronotum black or metallic green except small red spot on each anterior angle and each humeral angle (Fig. 32) (Mexico) .... *rufonotata* Stål
– Dorsal surface dark brown, black, or metallic green or blue; disc of pronotum, apex of coria, and basal angles of scutellum lacking red markings; anterolateral margins of pronotum usually yellow or red, rarely interrupted with dark markings 3
3(2). Dorsal surface metallic green, with medial longitudinal band on scutellum brick-red (Fig. 39) (Costa Rica, Panama) .... *verdana* McDonald
– Dorsal surface dark brown, black, or metallic green or blue, scutellum unicolorous, lacking red markings 4
4(3). Dorsal surface of head bicolorous, metallic green basally becoming orange to red distally at least on apices of juga (Fig. 46) (southern Mexico to Colombia and Venezuela) .... *splendens* (Blanchard)
– Dorsal surface of head unicolorous, dark brown, black, or metallic green or blue, lacking orange or red markings 5
5(4). Dorsal surface bright metallic green or blue; punctures on disc of pronotum relatively sparse, distance between adjacent punctures 3–5 times diameter of puncture 6
– Dorsal surface dark brown or black, rarely with slight green color; punctures on disc of pronotum relatively dense, distance between adjacent punctures at most about diameter of puncture 7
6(5). Reddish band along each anterolateral margin of pronotum usually infuscated near middle (Fig. 53); basal plates usually completely fuscous or black; ventral margin of pygophore in ventral view with small, medial, circular emargination (Fig. 54); posterior wall of pygophore in caudal view completely lacking black spicules (Fig. 55) (Mexico to Costa Rica) .... *infuscata*, new species
– Reddish band along anterolateral pronotal margins usually lacking infuscated areas

←

15, 16. *R. macdonaldi.* 15. Proctiger, dorsal view. 16. Proctiger, lateral view. 17, 18. *R. ecuadoriensis.* 17. Proctiger, dorsal view. 18. Proctiger, lateral view. Symbols: csb, constriction of spermathecal bulb; dfl, distal flange; dil, dilation of spermatheca; dp, digitiform process; pesr, proximal end of sclerotized rod; pfl, proximal flange; ppp, posterior projection of proctiger; sdil, sclerotized portion of dilation of spermathecal duct; spd, spermathecal duct; sr, sclerotized rod; spb, spermathecal bulb.



Figs. 19–24. Genital plates. 19. *Arocera* (*Euopta*) sp. 20. *A.* (*E.*) sp. 21. *A.* (*A.*) *aequinoxialis.* 22. *Rhyssocephala macdonaldi.* 23. *R. ecuadoriensis.* 24. *R. infuscata.* Symbols: bp, basal plate; gx2, gonacoxae 2; sp, spiracle; s10, sternite 10; 8pt, eighth paratergite; 9pt, ninth paratergite.

(Fig. 67); basal plates fuscous to black, becoming reddish basally; ventral margin of pygophore in ventral view with relatively large, subtriangular, medial emargination (Fig. 68); posterior wall of pygophore with small black spicules laterally (Fig. 69) (Panama and northwestern South America) .... *macdonaldi,* new species

7(5). Habitus relatively narrow, elongate, lateral margins of coria subparallel (Fig. 60); posterior wall of pygophore densely spiculate, with small spiculate horn on each side of middle produced dorsocaudad (Fig. 62); ventral margin of pygophore produced caudad, then curving dorsad apically, with shallow, medial, concave emargination in caudal view (Fig. 62) (Ecuador) .... *ecuadoriensis,* new species

– Habitus more broadly ovate, lateral margins of coria convex, not parallel (Figs. 25, 74, 81); posterior wall of pygophore spiculate, but lacking submedial spiculate horns (Figs. 76, 83), or lacking spicules completely (Fig. 27); ventral margin of pygophore produced caudad, but not curving dorsad apically and not medially emarginate in caudal view (Figs. 27, 76, 83) 8

8(7). Dorsal surface brown to dark brown, usually with a reddish cast; pronotal cicatrices usually darker, fuscous to black; lateral margins of pronotum and basal areas of coria usually dark orange to red; posteroventral surface of pygophore conically produced medially (Fig. 77) (southern Brazil) .... *rufolimbata* Stål

– Dorsal surface black, sometimes with a greenish cast; pronotal cicatrices usually

concolorous with surrounding area; lateral margins of pronotum and basal areas of coria usually yellow to pale orange; posteroventral surface of pygophore not conically produced medially 9

9(8). Posterior wall of pygophore with numerous black spicules except for medial glabrous depressed area and submarginal band along posterior margin of pygophore (Fig. 83) (northwestern South America) .... *inmaculata* (Pirán)

– Posterior wall of pygophore lacking black spicules (Fig. 27) (northwestern South America) .... *principalis* (Stål) (in part)

Rhyssocephala principalis (Stål, 1855), **New Combination**

Figs. 25–31, Map 3

Pentatoma principalis Stål, 1855:182; Stål, 1856:58.
Arocera principalis: Stål, 1861:140; Stål, 1862:107; Becker & Grazia-Vieira, 1971: 12; Grazia, 1984:73; Grazia, 1987:46, figs. 9–11.
Strachia principalis: Walker, 1867:316.
Arocera colombiana McDonald, 1984:116–118, figs. 72–79. **NEW SYNONYMY.**
Arocera splendens (of authors, not Blanchard): McDonald, 1984:103 (part).

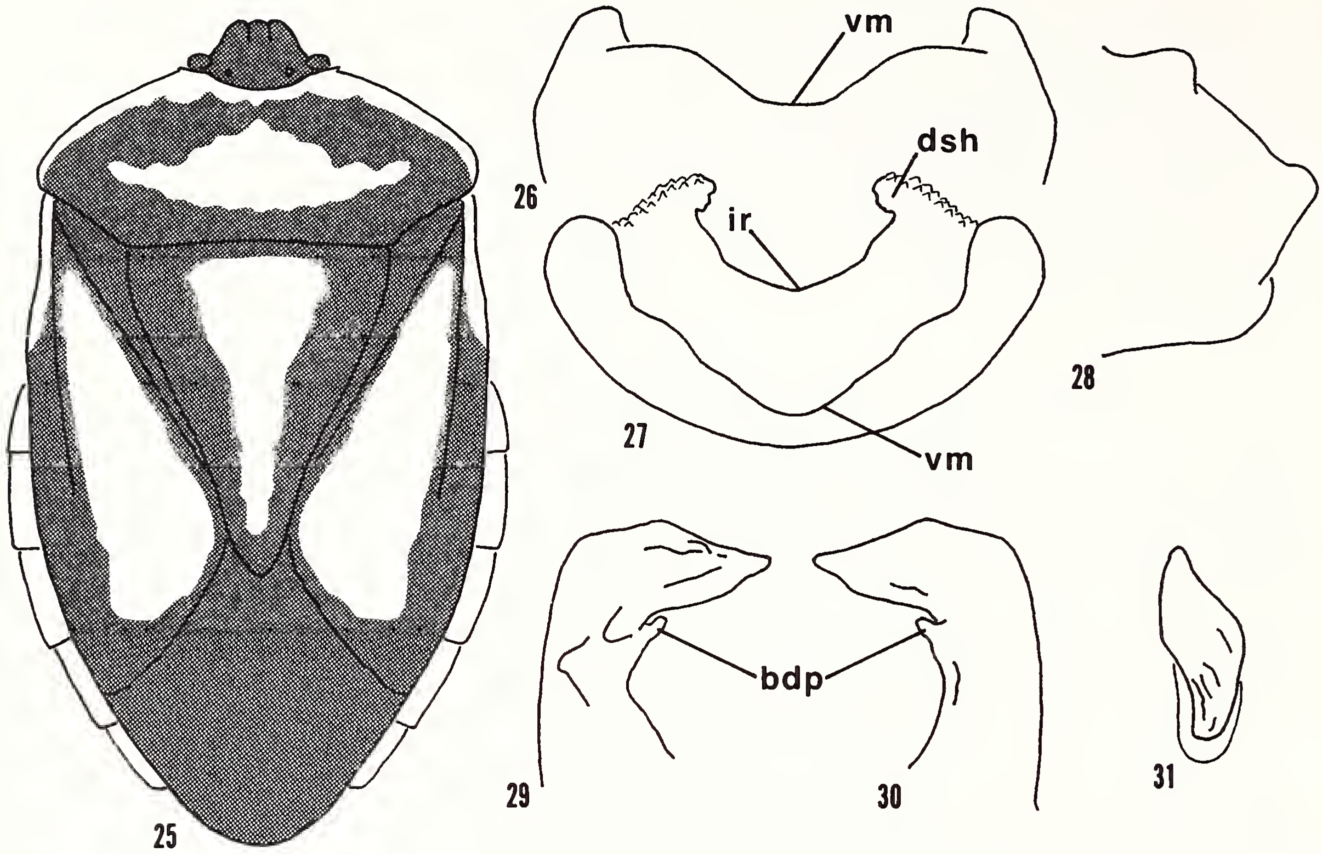
Diagnosis. Dorsal punctation minute, relatively dense, forming weak rugulose lines on pronotum and scutellum. Dorsal surface of color form I dark brown or black, sometimes with greenish cast; basal costal margin of each corium, anterior and often anterolateral margins of pronotum yellow to orange. Dorsal surface of color form II the same except discal areas of coria, scutellum, and pronotum brown, margined with black to metallic green (Fig. 25).

Dorsal surface of head black to dark metallic green; lateral jugal margins nearly straight, tapering to truncately rounded apex. Anterolateral margins of pronotum slightly convex. Connexiva usually concealed, usually with alternating areas of yellow or red and fuscous, sometimes entirely yellow or red (Fig. 25). Hemelytral membranes fumose.

Ventral surface black with yellow or orange spot near lateral margin of each abdominal segment, and another halfway between spiracle and middle of segment; some small yellow or orange areas present on thoracic pleura and head; pale areas sometimes more extensive, forming solid band along lateral margins of venter, or even venter mostly yellow with a few black areas around spiracles. Rostrum relatively short, at most reaching middle of hind coxae.

Ventral margin of pygophore produced caudad and slightly dorsad apically, in caudal view sinuously U-shaped (Fig. 27), in ventral view broadly and shallowly U-shaped (Fig. 26). Inferior ridge forming vertical wall, caudal surface tumescent medially, lacking black spicules (Fig. 27); dorsal margin of inferior ridge in caudal view broadly U-shaped (Fig. 27). Each paramere narrowly rounded apically in lateral and medial views (Figs. 29, 30); somewhat S-shaped in ectal view (Fig. 31). Basal plates fuscous to black. Spermathecal duct below proximal flange relatively thick.

Types. Stål (1855) described *Pentatoma principalis* from 1♀ specimen purportedly from Mexico. This specimen is identical to several ♀ specimens of color form I from Venezuela and Colombia. Although I have not examined any specimens of this species outside of South America except for the holotype specimen, I believe they are all conspecific. Either this specimen is mislabeled or this species is quite rare throughout



Figs. 25–31. *Rhyssocephala principalis*. 25. Habitus. 26–28. Pygophore. 26. Ventral view. 27. Caudal view. 28. Lateral view. 29–31. Right paramere. 29. Lateral view. 30. Medial view. 31. Ectal view. Symbols: bdp, basal digitiform process; dsh, dorsal spiculate horn; ir, inferior ridge; vm, ventral margin.

Central America into Mexico. The holotype was examined and is now conserved in the Naturhistoriska Museum, Stockholm, Sweden.

McDonald (1984) described *A. colombiana* from seven specimens from Venezuela and Colombia. The holotype and all six paratypes were examined. All seven specimens are of color form II, but I have compared ♂ specimens of both color forms and find no significant differences in the genitalia. The holotype is conserved in the United States National Museum of Natural History, Washington, D.C.

Specimens examined. 21 specimens; the one specimen with a date was collected in May; deposited in AMNH, BMNH, CAS, MACN, NHRS, USNM, ZMB. **MEXICO**[?]. **COLOMBIA:** *Boyacá:* Muzo. *Cundinamarca:* Fusagasugá; Oriente, Monterredondo. **VENEZUELA:** *Aragua:* Rancho Grande nr. Maracay. *Mérida:* Mérida.

Distribution. Known from Colombia and Venezuela (Map 3) and questionably Mexico.

Comments. McDonald (1984) considered this species to be a synonym of *R. splendens.* These two species can be separated by the distinctive genitalia.

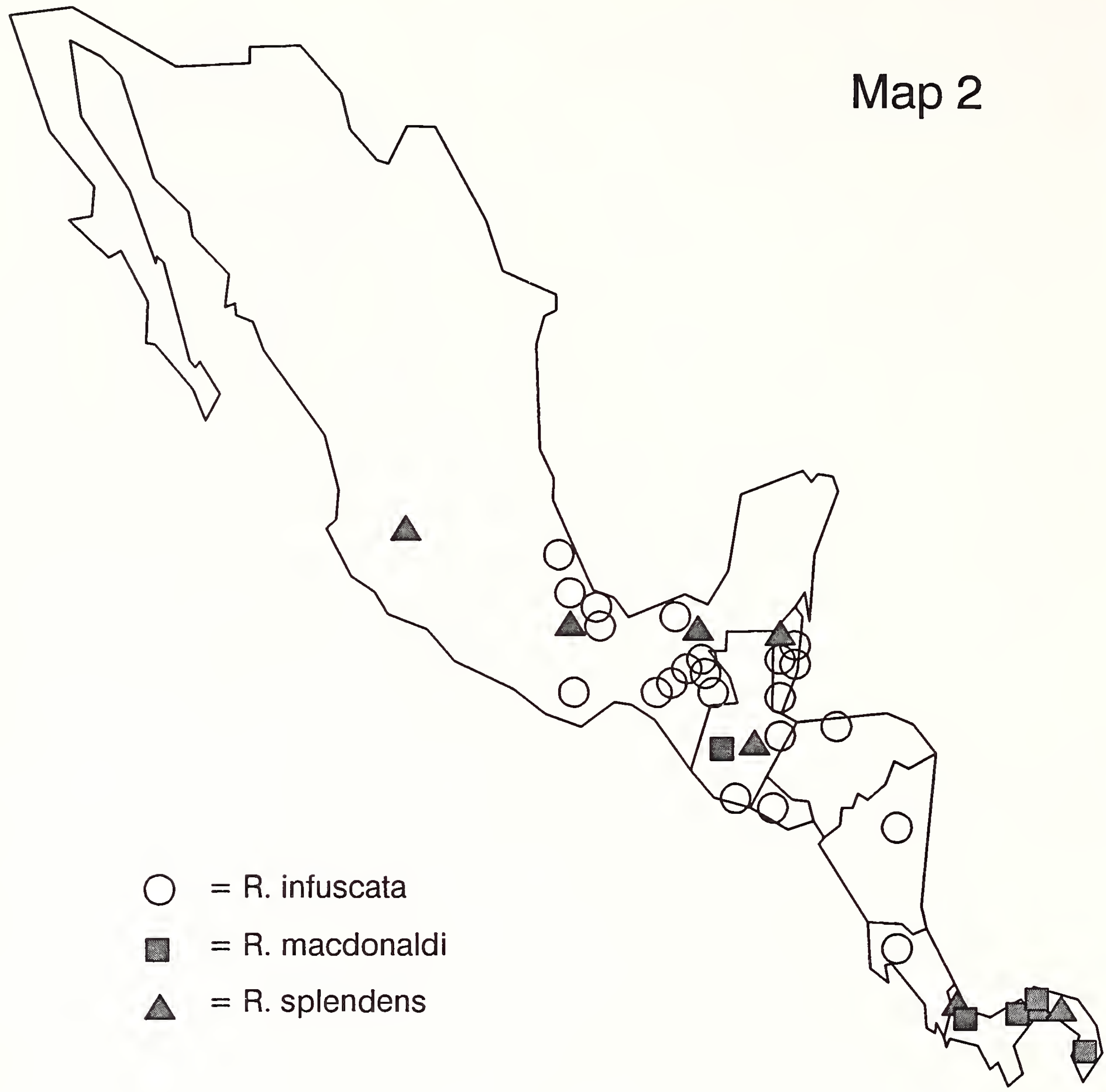
Specimens of color form II are easily recognized by their distinctive coloration. No other species of *Rhyssocephala* has extensive areas of brown bordered broadly or narrowly with black as in this species. Specimens of color form I are quite similar to specimens of *R. inmaculata* but can be separated from that species by differences in the male genitalia and by the shorter rostrum.

Map 1. *R. rufonotata* (○); *R. verdana* (■).

Rhyssocephala rufonotata (Stål, 1861), **New Combination**
Figs. 32–38, Map 1

Arocera rufonotata Stål, 1861:140; Distant, 1880:75, pl. 7, fig. 15; Distant, 1893: 338; Lethierry & Severin, 1893:159; Brailovsky & Barrera, 1982:237–238; McDonald, 1984:110–111, figs. 44–50.
Arocera (*Euopta*) *rufonotata:* Stål, 1872:38; Kirkaldy, 1909:110.
Strachia rufonotata: Walker, 1867:316.

Diagnosis. Dorsal coloration metallic green with some or all of the following red markings: small spot on each anterior and each humeral angle of pronotum; small spot on middle of pronotum; reniform spot on each basal angle of scutellum; triangular spot on each corium near apex of scutellum, and narrow marginal band along base of each corium (Fig. 32). Dorsal surface of head completely dark. Anterolateral



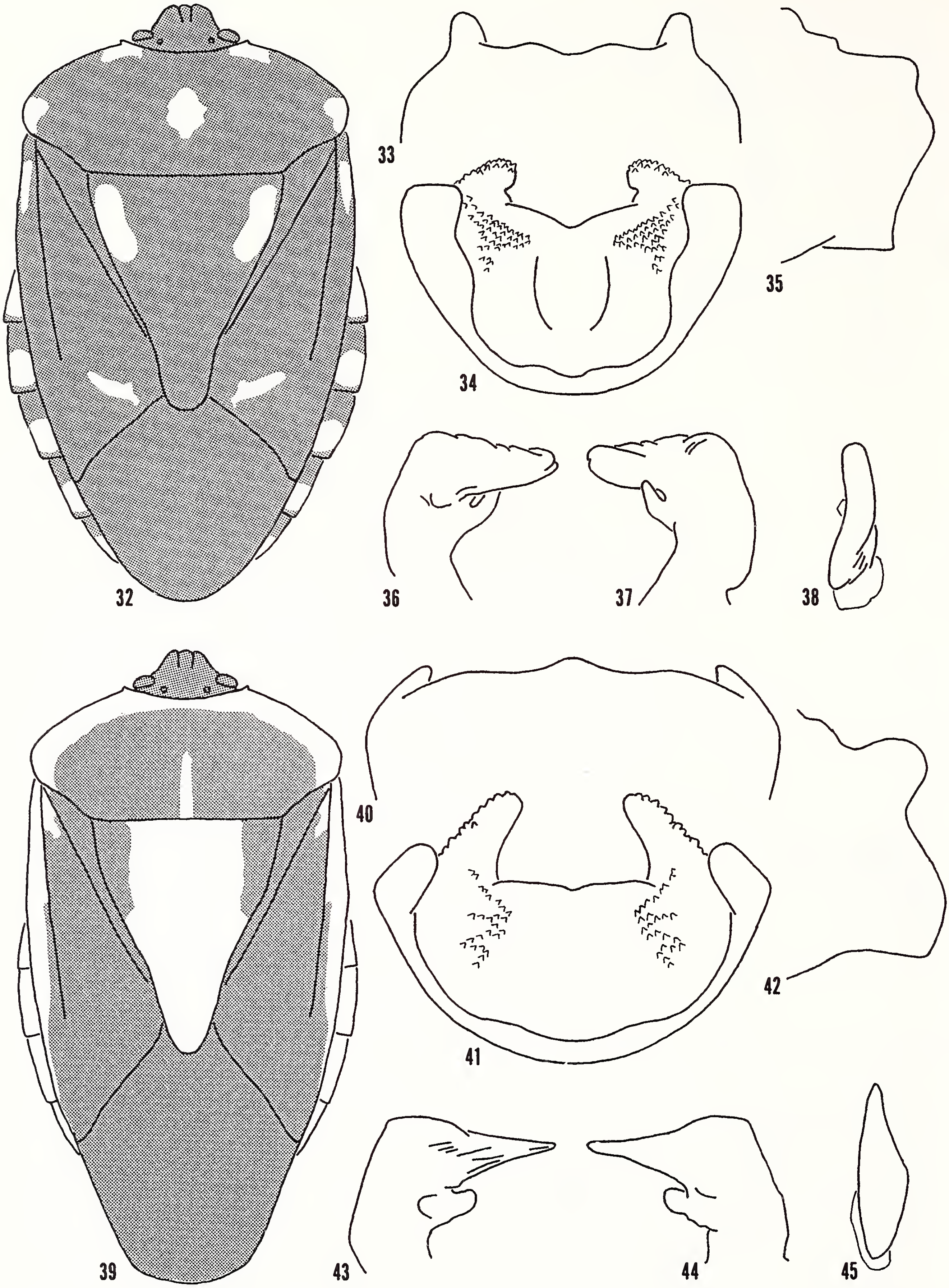
Map 2. *R. infuscata* (○); *R. macdonaldi* (■); *R. splendens* (▲).

margins of pronotum convex. Connexiva alternating black or metallic green with red (Fig. 32).

Ventral margin of pygophore in ventral view slightly sinuous, not emarginate at middle, lateral angles prominent (Fig. 33); in caudal view broadly U-shaped becoming sinuous laterally (Fig. 34). Inferior ridge broadly V-shaped in caudal view (Fig. 34). Surface of pygophore between ventral margin and inferior ridge with broad, vertical, tumescent band medially; each side depressed, a triangular area of small, black, spicules on each side dorsolaterally (Fig. 34); pygophore in lateral view sinuous (Fig. 35). Proctiger with posterior projections curving dorsad in lateral view. Each paramere with apex rounded in lateral and medial views (Figs. 36, 37); paramere-head in ectal view of uniform width, slightly arcuate (Fig. 38). Female genitalia typical for the genus.

Types. Stål (1861) described *A. rufonotata* from at least two specimens without designating a holotype or paratypes. Only one ♂ syntype was examined and is des-

Map 3. *R. inmaculata* (○); *R. principalis* (▲); *R. rufolimbata* (■).



Figs. 32–45. 32–38. *Rhyssocephala rufonotata.* 32. Habitus. 33–35. Pygophore. 33. Ventral view. 34. Caudal view. 35. Lateral view. 36–38. Right paramere. 36. Lateral view. 37. Medial view. 38. Ectal view. 39–45. *R. verdana.* 39. Habitus. 40–42. Pygophore. 40. Ventral view. 41. Caudal view. 42. Lateral view. 43–45. Right paramere. 43. Lateral view. 44. Medial view. 45. Ectal view.

ignated the lectotype. It is labeled (a) "Mexico" (b) "Sallé." (c) "Type." (d) "Typus" (e) "432 89" (f) "Riksmuseum Stockholm." The lectotype is conserved in the Naturhistoriska Riksmuseet, Stockholm, Sweden.

Specimens examined. 66 specimens collected from every month except January and March; deposited in AMNH, BMNH, CAS, CNC, DAR, DBT, EGER, HDEC, LHR, NHRS, TAMU, UNAM, USNM. **MEXICO:** *Chiapas:* Aguacero, 40 km W Tuxtla Gutierrez; Chorreodero Cyn, 5 mi E Chiapa de Corzo; 22 m S La Trinitaria; Municipio Angel Albino Corzo, along Río Custepec, below Finca Gadow; Palenque Hotel Tulija; Simojovel; Sumidero Cyn; Tapacuchula. *Colima:* Colima. *Distrito Federal. Guerrero:* Dos Arroyos; Tecpan. *Hidalgo:* nr. Jacala. *Oaxaca:* Municipio Candelaria Loxicha La Soledad. *San Luis Potosi:* 2 mi S Tamazunchale. *Tabasco:* Jalapa. *Tamaulipas:* Ciudad Victoria. *Veracruz:* Córdoba; Dos Amatas; El Vigia; Huatusco; Istmo de Tehantepec; Lake Catemaco; Los Tuxtlas Range; San Andres Tuxtla; Santa Martha Los Tuxtlas; Teocelo; Xalapa. **GUATEMALA:** Barcenos; Chicacao.

Distribution. Guatemala and eastern and southern Mexico (Map 1).

Comments. This species is easily recognized by the characteristic pattern of reddish spots on the dorsal surface.

Rhyssocephala verdana (McDonald, 1984), **New Combination**
Figs. 39–45, Map 1

Arocera verdana McDonald, 1984:114–116, figs. 67–71.
Arocera splendens (of authors, not Blanchard): Distant, 1880:74–75, pl. 7, figs. 13–14 (part).

Diagnosis. Dorsal surface metallic green with red markings along margins of pronotum and coria, and on median of scutellum (Fig. 39); punctures small, relatively dense.

Dorsal surface of head uniformly metallic green. Anterior and anterolateral margins of pronotum broadly bordered with red-brown; pronotal cicatrices and surrounding surface nearly impunctate. Scutellum dark red-brown, except marginal band along frena metallic green (Fig. 39); punctures obscure medially. Coria metallic green except basal to entire costal margins narrowly red-brown; connexiva uniformly red-brown (Fig. 39). Ventral surfaces dark metallic green to iridescent black except outer margins broadly bordered with red-brown.

Pygophore in ventral view slightly convex, somewhat produced medially (Fig. 40); in caudal view ventral margin broadly and sinuously U-shaped, produced caudad; inferior ridge forming vertical wall, medioventral surface concave, moderate amount of black spicules in middle of each side (Fig. 41); in lateral view dorsolateral angle obtusely produced (Fig. 42). Proctiger with posterior projections straight in lateral view, not curving dorsad. Each paramere with apex sharply acuminate in lateral and medial views (Figs. 43, 44), in ectal view paramere-head narrowly rounded apically (Fig. 45). Female genitalia typical for the genus.

Types. McDonald (1984) described *A. verdana* from 17 specimens from Panama and Costa Rica. The holotype is deposited in the United States National Museum of Natural History, Washington, D.C. The holotype and six paratypes of this distinctive species were examined.

Specimens examined. 23 specimens collected from April to August, and 31 January;

deposited in BMNH, CAS, DAR, DBT, HDEC, LHR, USNM. **COSTA RICA:** Cartago, 5 mi SE Moravia; Irazú; Juan Vinas. *Guanacaste. Puntarenas:* Monteverde. **PANAMA:** Boquete. *Chiriquí:* Barriles; 3 km W Cerro Punta; Renacimiento Sta. Clara; Volcan de Chiriquí.

Distribution. Known only from Costa Rica and Panama (Map 1).

Comments. This species is easily recognized by the broad red-brown medial band on the scutellum.

Rhyssocephala splendens (Blanchard, 1840), **New Combination**
Figs. 7, 8, 46–52, Maps 2, 4

Pentatoma splendens Blanchard, 1840:148.
Pentatoma splendida: Dallas, 1851:256.
Strachia splendida: Walker, 1867:316.
Arocera splendens: Stål, 1862:107; Distant, 1880:74–75, pl. 7, figs. 13–14 (part); Distant, 1893:337; Lethierry & Severin, 1893:159; Becker & Grazia-Vieira, 1971:12; Froeschner, 1981:68; Brailovsky & Barrera, 1982:238; McDonald, 1984:103–105, figs. 17–25 (part); Grazia, 1984:73; Grazia, 1987:45–46, figs. 6–8.
Arocera (*Euopta*) *splendens:* Stål, 1872:38; Kirkaldy, 1909:110.

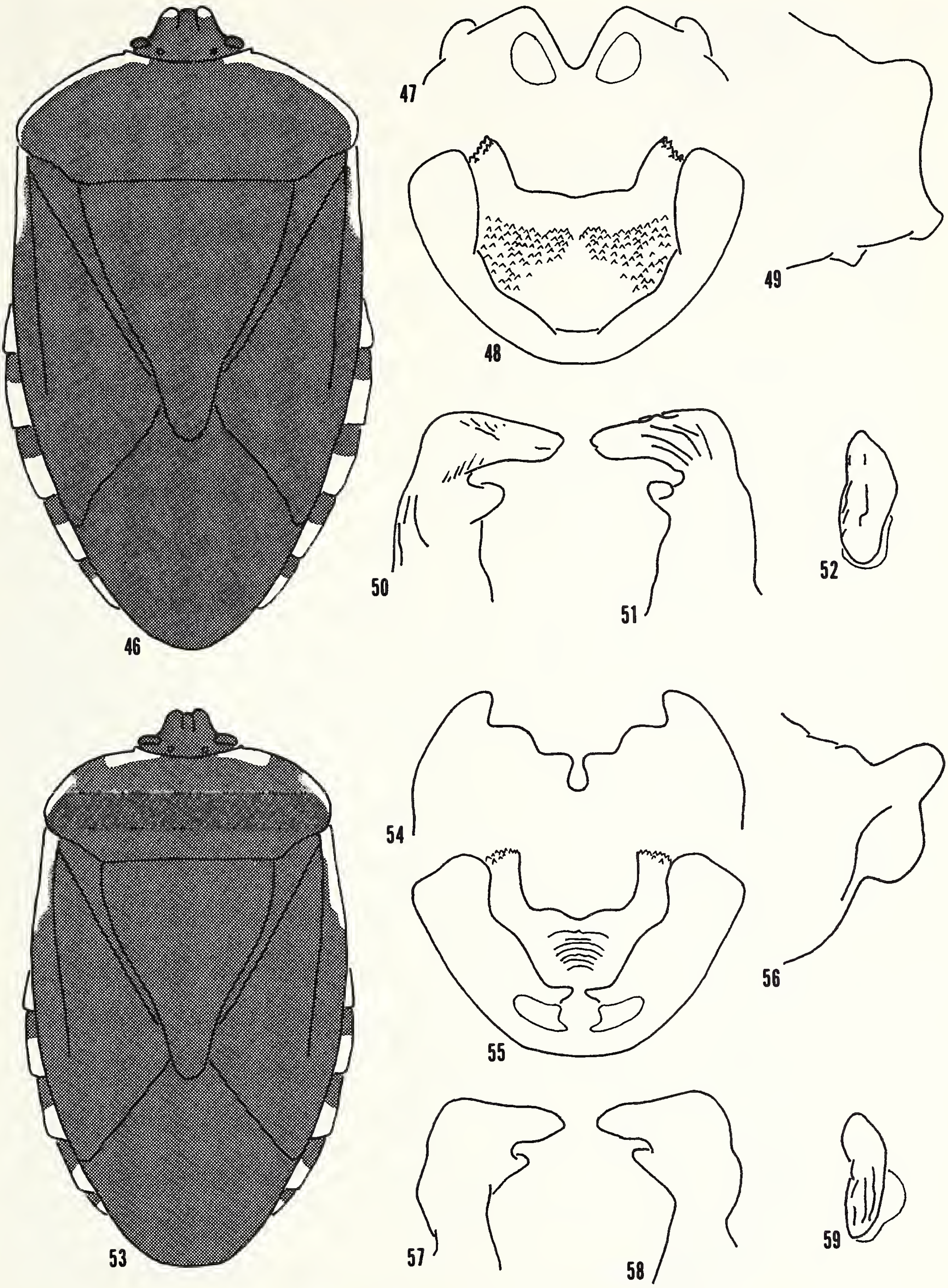
Diagnosis. Broadly oval, metallic green with yellow to red anterior and lateral markings (Fig. 46); punctation, at least on disc of pronotum, relatively sparse, minute.

Dorsal surface of head metallic green becoming yellow to orange laterally and apically (Fig. 46). Anterolateral margins of pronotum straight to slightly convex; reflexed portion nearly uniform in width becoming narrower near humeral angles; pronotal surface not depressed near anterolateral margins. Scutellum with a weak but distinct longitudinal carina from near apex to basal one-third.

Ventral margin of pygophore in ventral view with V-shaped emargination; distinct, circular depressed areas in surface on each side of V (Fig. 47); in caudal view ventral margin U-shaped, incised medially; inferior ridge forming vertical wall with triangular spiculate area on each side, ventromedial surface of wall distinctly concave, sometimes with small medial tumescence (Fig. 48). Posterior projections of proctiger relatively small, straight in lateral view. Each paramere with apex rounded in lateral and medial views (Figs. 50, 51); in ectal view paramere-head somewhat robust, rounded apically (Fig. 52). Spermathecal duct moderately coiled below proximal flange (Fig. 8).

Types. Blanchard (1840) described *Pentatoma splendens* from 1♂ and 1♀ specimen. Grazia (1987) designated the ♂ specimen lectotype and the ♀ specimen paralectotype. Both specimens were examined and the two specimens are not conspecific. The ♀ paralectotype is actually a specimen of the closely related species *R. macdonaldi*, as it lacks the pale coloration on the apex of the head. Both specimens are conserved in the Muséum National d'Histoire Naturelle, Paris, France.

Specimens examined. 49 specimens collected from 1 July to April; deposited in AMNH, BMNH, CAS, DBT, HDEC, MNHN, UNAM, USNM, ZMB. **MEXICO:** *Jalisco:* Tepatitlán. *Oaxaca:* San Mateo Yetla; Tuxtepec. *Tabasco:* Teapa. **BELIZE:** *Cayo:* El Cayo; Santa Familia. **GUATEMALA:** Panzós, Vera Paz. *Izabal:* Morales. **PANAMA:** Bugaba; Taboga Island. *Bocas del Toro. Canal Zone:* Madden Dam; Paraiso; Pedro Miguel. *Chepo:* Altos de Maje. **JAMAICA:** Montego Bay.



Figs. 46–59. 46–52. *Rhyssocephala splendens.* 46. Habitus. 47–49. Pygophore. 47. Ventral view. 48. Caudal view. 49. Lateral view. 50–52. Right paramere. 50. Lateral view. 51. Medial view. 52. Ectal view. 53–59. *R. infuscata.* 53. Habitus. 54–56. Pygophore. 54. Ventral view. 55. Caudal view. 56. Lateral view. 57–59. Right paramere. 57. Lateral view. 58. Medial view. 59. Ectal view.

Map 4. *R. ecuadoriensis* (■); *R. macdonaldi* (○); *R. splendens* (▲).

COLOMBIA: Felipe Ovalle. *Boyacá:* Muzo. *Huila:* Gigante. *Magdalena:* Aracataca; Santa Marta. **VENEZUELA:** Cumaragua. *Aragua:* El Limon; Rancho Grande. *Mérida:* Mérida. *Monagas:* Caripito. *San Felipe:* Aroa.

Distribution. Southern Mexico to northwestern South America (Maps 2, 4), with one record from Jamaica.

Comments. Males of this species are easily recognized by the distinctive genitalia; the V-shaped emargination in the ventral margin of the pygophore is diagnostic. Males and females can be identified by the pale areas on the apex of the head.

Rhyssocephala infuscata, new species
Figs. 9, 10, 24, 53–59, Map 2

Description. Dorsal surface metallic green with red markings along anterior and lateral margins (Fig. 53); punctation, at least on disc of pronotum, relatively sparse, minute; distance between adjacent punctures 2–5 times diameter of punctures.

Dorsal surface of head usually unicolorous, metallic green, extreme apex of each juga sometimes brownish. Dorsal surface of head distinctly wrinkled, rugose; vertex rugulose; apex of head truncately rounded; lateral jugal margins sinuous, reflexed, becoming slightly inflated apically. Antennae black.

Anterolateral margins of pronotum convex, reflexed, red except usually infuscated at middle (Fig. 53). Red marginal band continues onto basal one-fourth of each corium (Fig. 53). Scutellum usually with vague, longitudinal carina from near apex to basal one-third. Coria minutely punctured, posterior margins nearly straight, posterolateral angles narrowly rounded; hemelytral membranes metallic green. Connexiva usually alternating fuscous and red (Fig. 53).

Ventral surface reddish-brown to black with yellow to orange-red markings along lateral margins and on coxae, those on abdominal segments forming large macula in posterolateral angle of each sternite; some reddish markings on genital plates of female. Rostrum black, reaching onto base of abdomen, segment III longer than segment II. Ostiolar rugae elongate, curving slightly cephalad, reaching about two-thirds distance to lateral metapleural margin. Legs fuscous to black.

Ventral margin of pygophore in ventral view bisinuously U-shaped with small circular emargination medially (Fig. 54); in caudal view sinuously U-shaped, incised medially, posteroventral surface continuing ventrad below ventral margin with slightly depressed areas on each side of middle; inferior ridge forming vertical wall which lacks black spicules but has 5–8 weak transverse wrinkles medially (Fig. 55); inferior ridge in caudal view sinuously U-shaped (Fig. 55); pygophore in lateral view with posterolateral angles obtusely prominent (Fig. 56). Proctiger with posterior projections curving dorsad in lateral view. Each paramere with apex rounded in lateral, medial and ectal views (Figs. 57–59). Spermathecal duct nearly straight below proximal flange (Fig. 10).

Measurements. Total length 14.35–18.37 (14.98); total width 8.12–10.25 (8.52); medial length of pronotum 2.84–3.63 (3.12). Medial length of scutellum 6.15–7.49 (6.62); basal width 5.36–6.47 (5.52); width at distal end of frena 1.73–1.89 (1.88). Length of head 2.04–2.36 (2.15); width 3.03–3.53 (3.15); intraocular width 1.62–1.90 (1.62); intraocellar width 0.85–1.18 (0.88); ocellar diameter 0.22–0.29 (0.26); distance from ocellus to adjacent eye 0.28–0.29 (0.28). Length of segments I–V of antennae 0.63–0.96 (0.74), 1.29–1.47 (1.47), 1.99–2.37 (1.99), 3.02–3.39 (3.16), and

3.16–3.39 (3.24), respectively. Length of segments II–IV of rostrum 1.94–2.21 (2.13), 2.08–2.58 (2.43), and 1.41–1.66 (1.47), respectively.

Holotype. ♂ labeled "MEXICO: Chiapas Chorreodero Cnyn 5 mi E. Chiapa de Corzo IX-18-1985 B. Ratcliffe & C. Messenger." Deposited in the National Museum of Natural History, Washington, D.C.

Paratypes. 43♂♂ 68♀♀. (a) "Mexico" (b) "c" [ventral surface] (c) "Strachia splendida Walker's catal." (♀ BMNH); (a) "Mexico" (b) U.S.N.M. Acc. 18478" (♀ USNM); "R. Perez Acayucan Veracruz 10-VIII-75" (♀ UNAM); "Puente Nacional, Veracruz, Mexico August 24, 1967 H. R. Burke and J. Hafernik" (♂ LHR); "MEXICO, Ver. Cordoba X-22-1963 A. B. Lau" (♀ USNM); "Mex. Vera Cruz Cordoba, BL lite VIII-20-26-64 T. Taylor, Coll." (♀ CAS); (a) "Cordoba VC May 16, 05 Mex" (b) "FredkKnab Collector" (♂ USNM); (a) "Lake Catemaco Ver., Mex. 1000′ " (b) "VII-3-6-59 P.&C. Vaurie" (♂ AMNH); "MEXICO:Vera Cruz Lake Catemaco Area D. C. Robinson" (♂ EGER 2♀♀ LHR, TAMU); (a) "MEX. Lake Catemaco Ver. 9.VI.1969" (b) "H. F. Howden Collector" (♀ CNC); (a) "MEX. Santecomapan Ver. 10.VI.1969" (b) "H. F. Howden Collector" (♂ CNC); "MEXICO: Jalapa, Ver. VI-22-1947 Wegenre" (♂ AMNH); "MEXICO, Ver. Presidio X-28-1963 A. B. Lau" (♂ USNM); "San Andres Tuxtla Veracruz H. Brailovsky 22-VII-72" (♀ UNAM); (a) "EBSAT 28-C Los Tuxtlas Range Veracruz, Mexico VII-22-1963 D. C. Robinson" (b) "San Andreas Tuxtla" (2♀♀ EGER, TAMU); "México, Ver. Est. Biol. de Los Tuxtlas. Alt. 15-X-85 A. Ibarra." (♂ ♀ UNAM); "México, Ver. Est. Biol. de Los Tuxtlas. Alt. 15-XI-85" (2♀♀ UNAM); "México, Ver. Est. Biol. de Los Tuxtlas. Alt. 11a 17-XI-85 E. Ramírez" (♀ UNAM); "Los Tuxtlas Veracruz México 19-XII-76 S. Z. C." (♀ UNAM); "Los Tuxtlas Veracruz México 1-15/0/81 G. Ortega L." (2♀♀ UNAM); "C. El Vigia S. Tuxtla Veracruz 18-II-67" (♀ UNAM); "H. Perez Tuxtlas. Veracruz 30-X-75" (♀ USNM); "H. Perez Est. Los. Tuxtlas Veracruz 7-8.VIII.75 Noct" (♀ AMNH); (a) "Laguna Encautada Municipio de San Andrés Tuxtla Veracruz. MX" (b) "Alt. 350 m. viii 10, 1984 A. Chapp Foliage" (♀ EGER); "Est. Biol. Los Tuxtlas Veracruz Mexico 27-V-71 H. Gonzalez" (♂ UNAM); "San Andres Tuxtla Veracruz H. Brailovsky 11-I-72" (2♀♀ AMNH, USNM); "MEXICO, Veracruz: San Andres Tuxtla, Oct. 3 1947" (♀ AMNH); "Vera Cruz, Mex. Jaltipan X.23.70 R. Hancock, Coll." (♂ DAR); "J. J. Zertuche Campto. Cd. Alemán, Ver. 23-IX-1957" (♂ UNAM); "Villa Hermosa Tobasco, Mex. X-21-70 R. Hancock" (♂ CAS); "Mex. Oaxaca Temescal IX.19.71" (♀ CAS); "Palomares, Oaxaca Mex. IX/5-21/61 R&K Dreisbach" (♀ LHR); "Chiapas Mexico" (♀ CAS); "MEXICO: Chiapas Aguacero IX 1985 D. B. Thomas" (2♂♂ 3♀♀ DBT); "MEXICO: Chiapas Aguacero 10-VI-1986 D. B. Thomas" (♀ DBT); "Aqua Cera, 40 km west, Tuxtla Gutierrez, Chiapas, Mex. VI-21-87" (♂ ♀ DBT); "MEXICO, Chiapas 10 Km. S. Palenque 14-I-88 (D. B. Thomas Coll." (2♂♂ DBT); "MEXICO, Chiapas 10 Km. S. Palenque 24-VI-87 D. B. Thomas Coll." (♂ DBT); "MEXICO, Chiapas 10 Km. S. Palenque 11-X-86 D. B. Thomas Coll." (♀ DBT); "MEXICO, Chiapas 10 Km. S. Palenque 7-IX D. B. Thomas Coll." (♀ DBT); "MEXICO: CHIAPAS PALENQUE AUGUST 1988 D. B. THOMAS" (♂ DBT); "MEXICO: Chiapas Ruinas Palenque 20 August 1987 J. A. Shuey Colr." (♀ EGER); "MEXICO: Estado de Chiapas, Palenque Hotel "Tulija" 9.VI.1987 Stella E. Tatro" (♂ CAS); "La Esperanza Chiapas, Mex. IV.2.45 T. C. Schneirla" (♀ AMNH); (a) "Finca' La Isle' Chiapas, Mex." (b) "Presented by L. C. Reynolds" (2♀♀ CAS); "MEXICO: Chiapas Chicoasen IX-19-1985 B. Ratcliffe & C. Messenger" (2♂♂ ♀ DBT); "MEXICO: Chiapas Ocozocoautla Altitude 2700 ft 26–28.IX.1971 D. E. Breedlove"

(♀ CAS); "MEXICO, Chiapas Parque Laguna Belgica 10-VI-87 D. B. Thomas Coll." (♀ DBT); "3 km west, Cinco Cerros, Chiapas, Mexico VI-26-87" (♀ DBT); "MEXICO: CHIAPAS SIMOJOVEL MAY 1989 A.M. THOMAS" (♀ DBT); "R Nettel Col. Huixtla, Chis. 9.V.43" (♀ UNAM); "Mario Garcia Col. MEXICO: Chiapas Boca Lacantun. 24-V-84" (♀ UNAM); "MEXICO: Chiapas Boca Lacantun 24-V-84 M. Garcia" (♀ UNAM); "Ernesto Barrera Col. MEXICO: Chiapas Bonampak 20-22-V-84" (♀ UNAM); and "Mario García Col. MEXICO: Chiapas Bonampak 20-22-V-84" (♂ UNAM).

"BELIZE: Stann Creek District, Middlesex 28-II-1982 E. C. Welling, coll." (2♂♂ 2♀♀ EGER); "BELIZE: Stann Creek District, Middlesex 1-VI-1983 E. C. Welling, coll." (♀ EGER); "BELIZE, STANN CREEK VALLEY, MELINDA March 1, 1976 M. W. HETZ" (3♂♂ 2♀♀ DBT); "BELIZE, STANN CREEK VALLEY, MELINDA Feb. 16–March 16, 1976 M. W. HETZ" (♂ DBT); "BELIZE: STANN CREEK DIST. DANGRIGA 20 AUG 1988 D. B. THOMAS COLL." (♂ DBT); "British Honduras Middlesex Stann Creek dist. 29.IV.1965" (♀ CNC); "BELIZE: Belize 5-VI-1983 E. C. Welling, Coll." (♂ EGER); "Punta Gorda, British Hon Feb. 1931 J. J. White" (♂ USNM); "BRIT. HONDURAS. Cayo District Belmopan 26.VIII.71 Coll. R. O'Shea" (♀ BMNH); "Guatemala Dr. Ohaus G." (♂ ZMB); "GUATEMALA, Izabal, Ruinas de Quiriguá 24/25 August, 1974 E. M. Fisher, collr." (♂ DBT); "GUATEMALA: Quixal Alta Verapaz VII-1979 E. C. Welling, coll." (♂ ♀ EGER); "GUATEMALA: Quixal Alta Verapaz 600 m. 26–27-VII-1981. E. C. Welling, coll." (♀ EGER); (a) "GUATEMALA: San Jose IV-11-1951" (b) "Ross and Michelbacher Collectors" (♀ CAS); "Yepocapa Guatemala III-VI.45 H. Elishewitz" (♀ AMNH); (a) "Cayuga Guat. VI-'15" (b) "WmSchaus coll" (2♂♂ USNM); (a) "Cayuga Guat. IX-'15" (b) "Wm-Schaus coll" (♂ ♀ USNM); (a) "Cayuga Guat." (b) "Schaus and Barnes coll" (♂ USNM); "Morales, Guatemala Sep. 1929 J. J. White" (5♀♀ USNM); (a) "Morales Guatemala" (b) "J. J. White Sep 1928" (♂ USNM); (a) "San Salvador Salv. 1920 S. Calderon" (b) "no. 53" (♂ ♀ USNM); "HONDURAS: La Ceiba, July 1982 John Stamatov" (♂ AMNH); "NICARAGUA: Los Jinotepes V-1953 R.&C. Swain" (♂ AMNH); "C. R., Guan., La Pacifica nr. Cañas 22–26-V-84:E. Riley D. Rider & D. LeDoux" (♂ DAR); and "COSTA RICA, Guan. Prv. LaPacifica Nr Canas June 8, 1983 J. E. Wappes" (♀ LHR).

Distribution. Mexico to Costa Rica (Map 2).

Comments. This species is similar in coloration to *R. splendens* and *R. macdonaldi.* It can be separated from *R. splendens* by the lack of red or orange color on the apex of the head. In *R. macdonaldi,* the anterolateral margins of the pronotum are usually unicolorously red or yellow, whereas in *R. infuscata,* they are usually infuscated medially. The male genitalia are diagnostic in all three species.

Etymology. Most specimens of this species have the red submarginal band along the anterolateral margins of the pronotum infuscated medially. The species is named for that character.

Rhyssocephala ecuadoriensis, new species
Figs. 17, 18, 23, 60–66, Map 4

Description. Dorsal surface black with orange-red markings along anterolateral pronotal margins and on basal costal margins of coria (Fig. 60); dorsal punctation minute, dense.

Vertex of head somewhat tumid, roughened, with several transverse rugulose lines. Jugal surfaces diagonally rugulose; lateral jugal margins sinuous, not parallel, obtusely reflexed near apices; juga and tylus subequal in length. Tylus obscurely rugulose near base, tumid medially, declivant apically. Antennae black.

Pronotal surface with very small, obscure, rugulose lines between punctures; anterolateral margins distinctly reflexed. Anterolateral pronotal margins nearly weakly convex, humeral angles obtusely rounded, small obtuse tooth present in each anterior angle; anterior angle and anterolateral margins orange-red, becoming red-brown near each humeral angle. Posterolateral pronotal margin weakly sinuous; posterior pronotal margin weakly concave, nearly straight. Scutellum minutely punctured, a few obscure rugulose lines near base. Corium minutely and densely punctate; basal costal margin orange-red; posterior margin nearly straight; hemelytral membrane lightly fumose, veins subparallel. Connexiva narrowly exposed, anterior and posterior margins of each segment black with middle of each segment orange-red (Fig. 60).

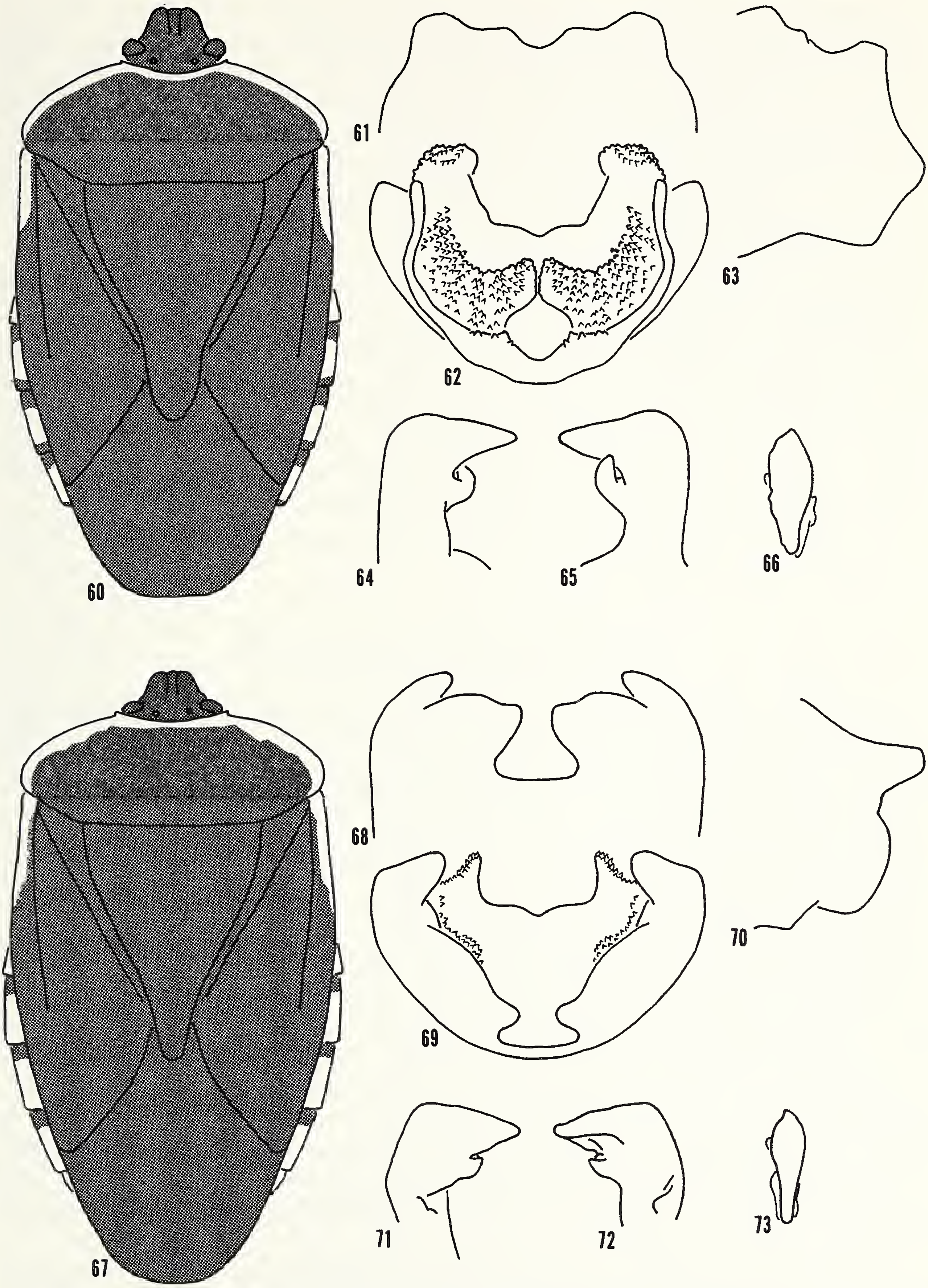
Ventral surface of head glabrous, orange-brown with fuscous to black markings around each antennifer and along lateral jugal margins. Rostrum black, reaching onto base of abdomen, segment II longer than segment III. Thoracic pleura fuscous to black with orange-red markings laterally, posteriorly and around coxae. Ostiolar rugae elevated, glossy, curving slightly cephalad, acuminate apically, reaching about two-thirds distance from ostioles to lateral metapleural margins. Legs black. Abdominal surface fuscous to black with obscure red markings submedially, more distinct orange-red spot just posterolateral to each spiracle, and U-shaped orange-red marking medially on last abdominal segment.

Inferior ridge of pygophore angularly bisinuate in caudal view (Fig. 62); ventral margin produced caudad then dorsad, forming excavated area between inferior ridge and ventral margin; surface of excavated area covered with small, black, setae-bearing tubercles except medially and along margin of inferior ridge; black spicules forming small horn on each side dorsomesially (Fig. 62). Ventral margin in caudal view bisinuate with U-shaped incision medially (Fig. 62); in ventral view bisinuate (Fig. 61); pygophore in lateral view sinuous, protruding caudad just below middle (Fig. 63). Proctiger with posterior projections straight in lateral view (Fig. 18). Each paramere with apex narrowly rounded in lateral and medial views (Figs. 64, 65), in ectal view paramere-head broader on apical than basal half, apex rounded (Fig. 66). Female genitalia typical for the genus.

Measurements. Total length 14.19–18.14 (15.14); total width 8.36–10.25 (8.75); medial length of pronotum 2.30–3.47 (3.00). Medial length of scutellum 6.15–7.81 (6.94); basal width 5.20–6.15 (5.52); width at distal end of frena 1.73–2.21 (1.89). Length of head 2.13–2.37 (2.15); width 3.09–3.48 (3.26); intraocular width 1.66–1.88 (1.71); intraocellar width 0.92–1.07 (1.03); ocellar diameter 0.23–0.29 (0.26); distance from ocellus to adjacent eye 0.28–0.31 (0.29). Length of segments I-V of antennae 0.77–0.83 (0.77), 1.25–1.64 (1.47), 2.12–2.51 (2.17), 2.36–2.87 (2.54), and 2.43–2.65 (2.47), respectively. Length of segments II–IV of rostrum 1.94–2.50 (2.04), 1.88–2.28 (1.93), and 1.24–1.55 (1.32), respectively.

Holotype. ♂ labeled (a) "ECUADOR, El Oro: W. of Santa Rosa just S. Machala II-18-1965" (b) "L. E. Pena Collector" (c) "*Arocera splendens* (Blanch.) Det. F. J. D. McDonald." Deposited in the American Museum of Natural History, New York.

Paratypes. 7♂♂, 7♀♀. Labeled as holotype (2♂♂ 2♀♀ AMNH); "ECUADOR Santo



Figs. 60–73. 60–66. *Rhyssocephala ecuadoriensis.* 60. Habitus. 61–63. Pygophore. 61. Ventral view. 62. Caudal view. 63. Lateral view. 64–66. Right paramere. 64. Lateral view. 65. Medial view. 66. Ectal view. 67–73. *R. macdonaldi.* 67. Habitus. 68–70. Pygophore. 68. Ventral view. 69. Caudal view. 70. Lateral view. 71–73. Right paramere. 71. Lateral view. 72. Medial view. 73. Ectal view.

Domingo de los Colorados, Pichincha 7 February 1958 R. W. Hodges, 2000′" (♂ LHR); (a) "Light" (b) "Guayaquil ECUAD 17 April 1920 Cornell U. Exped Lot 607 Sub 25" (c) "Cornell Univ. Expedition Lot 607 Sub 25" (♂ AMNH); (a) "ECUADOR: Balao Chico, 60km S. Guayaquil Guayas Prov., Jan.-1964" (b) "L. E. Pena Collector" (♀ AMNH); (a) "ECUADOR Puna Is. XI-9-1950" (b) "A E Michelbacher" (♀ CAS); "ECUADOR ESMERALDAS CUPA 30-I-1982 Lg. D. POVEDA" (♂ BMNH); "ECUADOR PICHINCHA PTO QUITO 3-XII-83 LEG: E. FIALLO" (♂ BMNH); (a) "Tropical rainforest general collecting" (b) "ECUADOR, Pichincha, Puerto Quito, 750m. x–xi. 1982 G. Onore" (♂ ♀ BMNH); "S. Domingo de los Colorados 29–Nov-1975 Floreano Merino" (♀ BMNH); and (a) "7207" (b) "Guayaquil. Reisj." (♀ ZMB).

Distribution. Known only from Ecuador (Map 4).

Comments. The fuscous to black dorsal coloration and dense pronotal punctation places this species near *R. inmaculata, R. principalis,* and *R. rufolimbata.* It is, however, differently shaped than those species. *Rhyssocephala ecuadoriensis* is more elongate and narrow, resembling *R. splendens, R. macdonaldi,* and *R. infuscata* in shape. These last three species are all distinctly metallic-green or blue and have the pronotal disc sparsely punctate; the male genitalia are also diagnostic.

Etymology. This species is named for Ecuador, the country from which all of the specimens in the type series were collected.

Rhyssocephala macdonaldi, new species

Figs. 15, 16, 22, 67–73, Maps 2, 4

Description. Dorsal surface metallic green or blue with yellow to red markings along anterolateral pronotal margins and on basal costal margins (Fig. 67); dorsal punctation minute, dense, except pronotal disc sparsely punctate; distance between punctures on pronotal disc 3–5 times diameter of puncture.

Vertex of head slightly tumid, distinctly wrinkled or rugulose. Jugal surfaces diagonally rugose; lateral jugal margins sinuous, not parallel, slightly reflexed, becoming inflated distally; apex of head truncately rounded, juga and tylus subequal in length. Dorsal surface of head usually unicolorous, sometimes slight red-brown coloration along creases between juga and tylus. Antennae black.

Anterolateral margins of pronotum slightly convex, reflexed; submarginal red band entire, uninterrupted medially by fuscous; humeral angles rounded; anterior angles each armed with small tooth (Fig. 67). Scutellum minutely punctured, a few weak rugulose lines basally and laterally; sometimes with vague, medial, longitudinal carina from near apices of frena to basal third, sometimes with circular depressed area on base of scutellar tongue. Coria minutely punctured, posterior margins nearly straight, posterolateral angles narrowly rounded; hemelytral membranes metallic green, veins subparallel. Connexiva narrowly exposed, usually red alternating with fuscous along each anterior margin (Fig. 67).

Ventral surface red-brown to fuscous with red-orange markings near bucculae, on coxae, and along lateral margins. Rostrum fuscous to black, reaching onto base of abdomen, segment III longer than segment II. Ostiolar rugae elongate, curving slightly cephalad, reaching about two-thirds of distance from ostioles to lateral metapleural margins. Legs fuscous to black.

Ventral margin of pygophore in ventral view sinuous with large flask-shaped emar-

gination medially (Fig. 68); in caudal view ventral margin sinuously U-shaped, incised medially; inferior ridge forming vertical wall with moderate amount of black spicules laterally, broadly U-shaped with medial part weakly concave (Fig. 69); in lateral view posterolateral angles of pygophore truncate, prominent (Fig. 70). Proctiger with posterior projections curving dorsad in lateral view (Fig. 16). Each paramere narrowly rounded in lateral and medial views (Figs. 71, 72), in ectal view paramere-head broader on apical half than basal half, nearly acute apically (Fig. 73).

Measurements. Total length 14.35–17.66 (14.74); total width 7.73–9.54 (7.96); medial length of pronotum 2.68–3.08 (2.76). Medial length of scutellum 5.99–7.25 (6.15); basal width 4.81–6.15 (5.13); width at distal end of frena 1.58–1.89 (1.73). Length of head 1.99–2.37 (2.04); width 2.95–3.20 (3.04); intraocular width 1.47–1.67 (1.55); intraocellar width 0.85–0.88 (0.85); ocellar diameter 0.29–0.33 (0.29); distance from ocellus to adjacent eye 0.18–0.29 (0.29). Length of segments I–V of antennae 0.66–0.85 (0.74), 1.21–1.44 (1.21), 1.74–2.21 (1.86), 2.65–3.16 (2.91), and 2.70–3.13 (2.83), respectively. Length of segments II–IV of rostrum 1.93–2.32 (1.99), 2.06–2.72 (2.06), and 1.38–1.91 (1.44), respectively.

Holotype. ♂ labeled "VENEZUELA RanchoGrande 17-I-66." Deposited in the National Museum of Natural History, Washington, D.C.

Paratypes. 29♂♂, 34♀♀. Labeled as holotype except "18-I-66" (2♂♂ USNM); labeled as holotype except "24-I-66" (♂ USNM); labeled as holotype except "I-66" (♂ USNM); (a) "VENEZUELA: Guanare, estado Portuguesa IX-10 to 13-1957" (b) "Borys Malkin Collector" (♂ ♀ CAS); (a) "1982" (b) "Agua Santa, Trujillo, Venezuela" (c) "HPittier Coll" (♀ USNM); "Valera, Venez. 1800 ft EPdeBellard" (♀ USNM); "Merida Venezuela" (♂ ♀ CAS); (a) "46701" (b) "VENEZUELA: Rancho Grande nr. Maracay VI-29-1946" (♂ AMNH); "Venezuela Kummerow" (3♂♂ 6♀♀ ZMB); "Venezuela F. Kummerow S." (2♂♂ 2♀♀ ZMB); Venezuela Valencia F. Kummerow S. V." (3♀♀ ZMB); "LA GUAYRA leg OTTO Nr. 505" (♂ ♀ ZMB); "Barinitas. 500m. Edo. Barinas Venezuela 15-V-66 Gadon" (♂ UNAM); (a) "Espinal Colombia So. Amer." (♀ USNM); (a) "Medellin Colombia" (b) "FlGallegoM Col No 86, Let. Jan. 44" (♂ USNM); "Magdalena Colombia, S A June 1936" (♂ LHR); (a) "COLOMBIA: Rio Leon Chigorodo.Ant. 11–17 Apr 1965" (b) "H. Marin Collector" (♂ USNM); "Aracataca, Mgd. Colombia V-13 Darlington 28" (4♀♀ AMNH); "Aracataca, Mgd. Colombia V-12 Darlington 28" (♀ AMNH); "Muzo SA Colombia" (♀ CAS); "S. Columbien Mocoa 5-6-22 am Putumaya W. Hopp S. G." (♀ ZMB); "Santa Marta Colombia Apr. 28, 1925" (♀ USNM); "Rio Palenque, Ecuador Los Rios Prov.-J. Longino 18-VI-74" (♂ EGER); "ECUADOR: Pichincha Prov. Tinalandia; 12 km. E. Sto. Domingo de los Colorados. ca. 2500 ft., 11–17-V-1986. J. E. Eger, coll." (♀ EGER); "Ecuador Pichingha, 15km E Sn. Domingo 31-X-74 at lights" (♀ HDEC); (a) "Ecuador Pichingha, 15km E Sta. Domingo" (b) "Collection of H. D. Engleman Jeff Balev Collector 23-IV-75" (♀ HDEC); "ECUADOR PICHINCHA-X TOACHI 1983 Legit: G. Onore" (♀ BMNH); "ECUADOR, Pichincha, Puerto Quito, 750m. x–xi. 1982 G. Onore" (♂ BMNH); (a) "Amazonian rain forest" (b) "ECUADOR: Pichincha Puerto Quito. vi. 1982. G. Onore" (♀ BMNH); (a) "GatunCZ Pan 7-V-11" (b) "A H Jennings Collector" (♀ USNM); "Gatun Spillway Pan. Canal Zone 11.IV.76 Col: D. Engleman" (♂ LHR); "Gatun Spillway Pan. Canal Zone 25 VI 74 Col: D. Engleman" (♂ HDEC); "Gatun Spillway Pan. Canal Zone 30-VII-74 Col: D. Engelman" (2♂♂ HDEC, ♂ ♀ LHR); "PANAMA: ZONA DEL CANAL; Barro Colorado Island. July 1980. R.

Silberglied/A. Aiello." (♀ USNM); PANAMA BOCAS DEL TORO 10KM NE FORTUNA DAM 3400' MAY 23–26 1984 E. GIESBERT, COLL." (♀ HDEC); "Cerro Campana 800 M; Dist. Chame, PANAMA 3.VI.81 Col. H. D. Engleman" (♂ HDEC); "PANAMA, DARIEN PR. 23KM. E CAÑANZAS MAY 16 1982 E. GIESBERT, COLL." (2♂♂ HDEC); (a) "Olas de Moka Dept. Sosola Guatemala IX-08" (♂ USNM); (a) "JAMAICA? dead in airplane at Miami, Fla." (b) "L. A. McLain 64-20306" (♂ USNM).

Distribution. Guatemala to northwestern South America, with one questionable record from Jamaica (Maps 2, 4).

Comments. This species is similar in appearance to *R. splendens* and *R. infuscata.* It can be separated from both species by the distinctive male genitalia. In *R. splendens,* the medial emargination of the ventral margin of the pygophore is V-shaped, and in *R. infuscata,* the medial emargination is small and circular. In *R. macdonaldi,* the medial emargination is larger and flask-shaped. It can also be separated from *R. splendens* by the lack of orange or red coloration on the apex and lateral margins of the head. It can usually be separated from *R. infuscata* by the lack of infuscation of the red submarginal band along the anterolateral pronotal margins.

Etymology. This species is named in honor of F. J. D. McDonald, who has contributed much to the knowledge of this genus and many other pentatomoid genera.

Rhyssocephala rufolimbata (Stål, 1872), **New Combination**
Figs. 74–80, Map 3

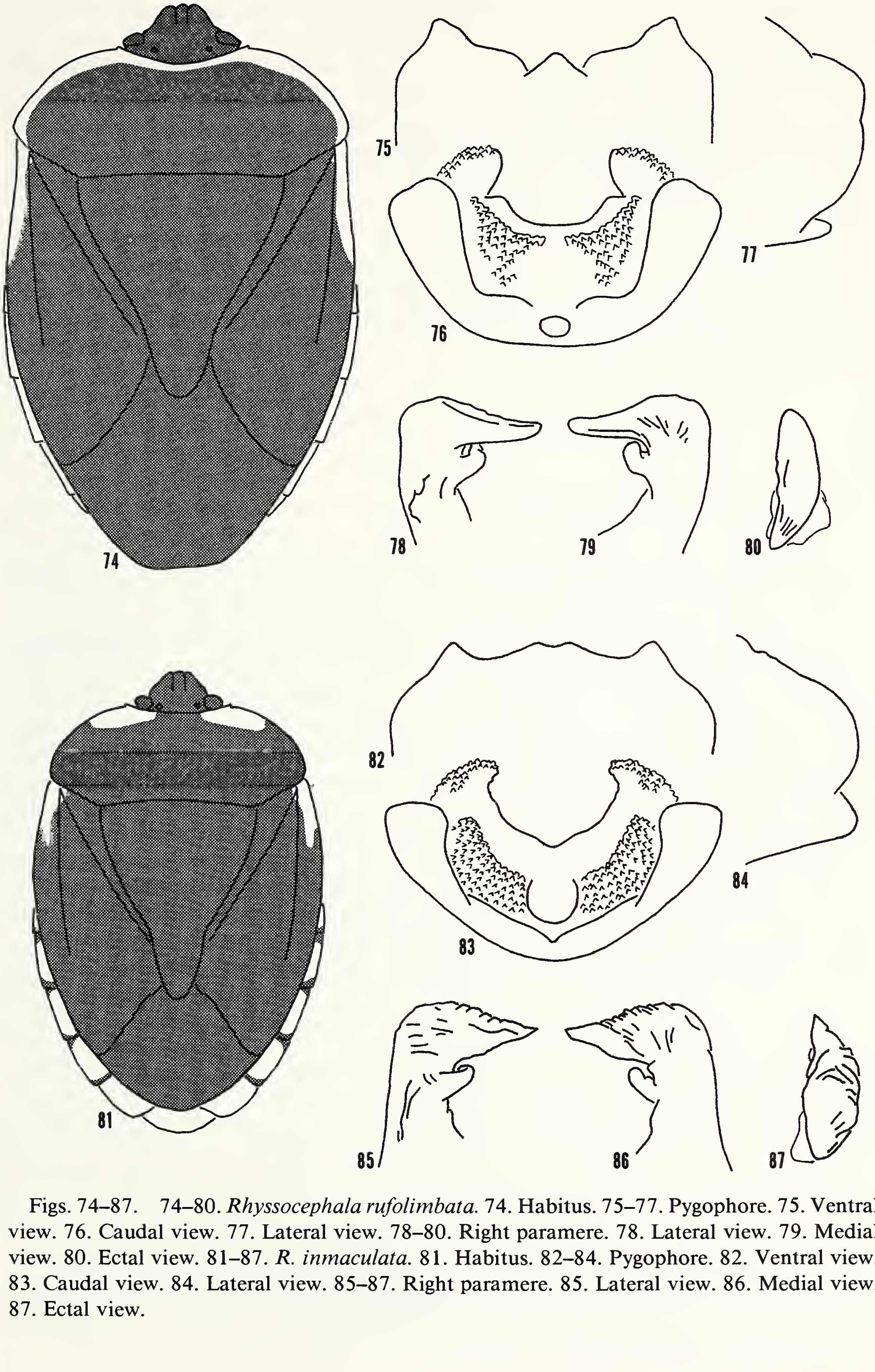
Arocera (*Euopta*) *rufolimbata* Stål, 1872:38; Kirkaldy, 1909:110.
Arocera rufolimbata: Lethierry & Severin, 1893:159; Monte, 1945:269; Grazia, 1977: 163; McDonald, 1984:111–112, figs. 51–55.

Diagnosis. Broadly ovate. Dorsal surface castaneous to fuscous, becoming black around pronotal cicatrices, anterior and anterolateral pronotal margins usually pale orange-red, continuing for short distance along lateral costal margin of each corium (Fig. 74); dorsal punctation minute, relatively dense.

Dorsal surface of head dark red-brown to black; lateral jugal margins slightly sinuous; apex truncately rounded. Antennae black. Anterolateral margins of pronotum distinctly convex. Connexiva narrowly exposed, usually entirely red (Fig. 74), rarely with small amount of black along intersegmental sutures. Hemelytral membranes fumose.

Ventral surface of head red except narrow margin fuscous. Rostrum completely black, reaching onto base of abdomen. Thoracic pleura fuscous to black except lateral margins and surface surrounding each coxa red. Ventral surface of abdomen with alternating bands or rows of spots of red and black. Legs entirely fuscous.

Inferior ridge of pygophore forming vertical wall with spiculate triangular area on each side of meson, dorsally ending abruptly in slightly elevated denticulate ridge paralleling pygophoral opening (Fig. 76). Posterior surface of pygophore produced caudad into U-shaped ridge becoming obsolete ventrally near middle; posteroventral surface with distinct cone-shaped protuberance medially (Fig. 76); pygophore in lateral view sinuous, posteroventral protuberance clearly visible (Fig. 77). Proctiger with posterior projections straight, not curving dorsad in lateral view. Each paramere somewhat acuminate apically, apex narrowly rounded in lateral and medial views



Figs. 74–87. 74–80. *Rhyssocephala rufolimbata.* 74. Habitus. 75–77. Pygophore. 75. Ventral view. 76. Caudal view. 77. Lateral view. 78–80. Right paramere. 78. Lateral view. 79. Medial view. 80. Ectal view. 81–87. *R. inmaculata.* 81. Habitus. 82–84. Pygophore. 82. Ventral view. 83. Caudal view. 84. Lateral view. 85–87. Right paramere. 85. Lateral view. 86. Medial view. 87. Ectal view.

(Figs. 78, 79); in ectal view paramere-head nearly uniform in width, broadly rounded apically (Fig. 80).

Types. The holotype ♀, which was examined, is deposited in the Naturhistoriska Riksmuseet, Stockholm, Sweden.

Specimens examined. 15 specimens collected from 1 October to March; deposited in BMNH, CAS, LHR, NHRS, USNM, ZMB. **BRAZIL:** *Rio de Janeiro:* Petrópolis. *Santa Catarina:* Corupá; Nova Teutônia; Rio Vermelho; Theresopolis. *São Paulo:* São Paulo.

Distribution. Known only from southern Brazil (Map 3).

Comments. This species is very similar to *A. inmaculata* but can be separated from that species by differences in the male genitalia and usually by the coloration of the anterior and lateral borders of the dorsum which is usually red in *A. rufolimbata* and usually pale yellow in *A. inmaculata.*

Rhyssocephala inmaculata (Pirán, 1963), **New Combination**
Figs. 81–87, Map 3

Pharypia inmaculata Pirán, 1963:109–111, figs. 5–6.
Arocera inmaculata: Grazia, 1986:52.

Diagnosis. Broadly oval. Dorsal surface black to very dark metallic green with pale yellow markings along anterolateral pronotal margins, on basal costal margin of each corium, and on connexiva (Fig. 81); dorsal punctation minute, dense.

Lateral jugal margins sinuous, not parallel, slightly inflated apically; juga and tylus subequal in length. Tylus transversely rugulose on base, elevated medially, declivant apically. Antennae black. Anterolateral pronotal margins slightly convex; humeral angles broadly rounded; small obtuse tooth in each anterior pronotal angle; posterolateral pronotal margins nearly straight, slightly concave; posterior margin nearly straight. Coria minutely and densely punctate; basal costal margins pale yellow; posterior margins nearly straight; hemelytral membranes fumose, veins subparallel. Connexiva completely pale yellow, or incisures bordered both anteriorly and posteriorly with fuscous (Fig. 81).

Ventral surface of head nearly glabrous, fuscous with pale yellow area along base of bucculae in male, pale yellow with fuscous markings near jugal margins in females. Rostrum black, reaching onto base of abdomen. Thoracic pleura black with anterolateral margin of propleura and ventral corial surfaces pale yellow in male; thoracic pleura yellow-orange with medial fuscous areas in females. Legs black, except inferior and superior surfaces of femora sometimes streaked with yellow. Abdominal surface black with submedial and lateral pale yellow spot on each segment, becoming more extensive on last segment in male; entire abdominal surface pale yellow in females.

In caudal view inferior ridge well-developed, sinuously V-shaped (Fig. 83); ventral margin sinuously U-shaped, thickened medially, produced caudad; surface between inferior ridge and ventral margin with numerous, small, black, seta-bearing tubercles, especially on transverse ridge paralleling inferior ridge; field of setose tubercles interrupted medially by sunken, glabrous area (Fig. 83). Ventral margin in ventral view bisinuous, somewhat produced, but not excised medially (Fig. 82); pygophore in lateral view emarginate below middle (Fig. 84). Posterior projections of proctiger nearly straight in lateral view. Each paramere with apex acutely pointed in lateral, medial, and ectal views (Figs. 85–87).

Types. Pirán (1963) described *Pharypia inmaculata* from 5♂ and 11♀ specimens. The holotype specimen was not located, but 2♂ and 9♀ paratype specimens were examined. Nine of the 11 specimens are conserved in the Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina. The other two paratypes are conserved in the Universidad Nacional de La Plata, Argentina.

Specimens examined. 26 specimens collected from 25 July [only one specimen had a collection date]; deposited in BMNH, CAS, DAR, MACN, MLPA, NCSU, USNM, ZMB. **COLOMBIA:** *Boyacá:* Muzo. *Cundinamarca:* Fusagasugá. *Meta:* Villavicencio. **PERU:** Agualani; Carabaya; La Merced, Valle Chancha mayo; Mont. Phillippi; Tozuzo. **BOLIVIA:** *Santa Cruz:* Río Espejo, Prov. Ibañez.

Distribution. Colombia, Peru, and Bolivia (Map 3).

Comments. This species is most closely related to *A. rufolimbata.* Specimens of *A. rufolimbata* usually have the body narrowly margined with red, while in specimens of *A. inmaculata* this narrow margin is usually pale yellow. The male genitalia are also distinctive.

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BMNH—British Museum (Natural History), London, W. R. Dolling
CAS—California Academy of Sciences, San Francisco, P. H. Arnaud
CNC—Canadian National Collections, Ottawa, Canada, M. D. Schwartz
DBT—D. B. Thomas personal collection, Tuxtla Gutierrez, Mexico
EGER—J. E. Eger personal collection, Tampa, Florida
HDEC—H. D. Engleman personal collection, Coco Solo, Panama
LHR—L. H. Rolston personal collection, Baton Rouge, Louisiana
MACN—Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires, A. O. Bachman
MLPA—Facultad de Ciencias Naturales y Museo, La Plata, Argentina, R. A. Ronderos
NCSU—North Carolina State University, Raleigh, R. L. Blinn
MNHN—Muséum National D'Histoire Naturelle, Paris, France, D. Pluot-Sigwalt
NHRS—Naturhistoriska Riksmuseet, Stockholm, Sweden, P. Lindskog
TAMU—Texas A&M University, College Station, E. G. Riley
UNAM—Universidad Nacional Autónomia de Mexico, Mexico City, H. Brailovsky
USNM—United States National Museum of Natural History, Washington, D.C., T. J. Henry
ZMB—Zoologisches Museum, Berlin, J. Deckert

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TWO NEW SPECIES OF TERATEMBIIDAE (EMBIIDINA) FROM ARGENTINA

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Abstract.—Both sexes of two new species of Teratembiidae from Argentina, are described and illustrated. *Oligembia mini,* n. sp. is closest to *Oligembia bicolor* Ross, 1944. *Diradius erba,* n. sp. is closest to *Oligembia unicolor* Ross, 1944 (which seems to belong to *Diradius*).

Embiidina is a group well defined by a series of morphological and behavioral characters (Ross, 1970; Hennig, 1981). Most of the characters considered important for species recognition in this group refer to male characters, mainly terminalia, coloration, form and size of eyes, wing venation, and size and number of papillae on the hind basitarsus. The only female characters mentioned in the literature to distinguish species are total length, coloration, and number of papillae on the hind basitarsus (Ross, 1944, 1970). However, the hind basitarsus chaetotaxy, and the form and position of papillae in females (previously illustrated for males of some species, in papers by Krauss, 1911; Davis, 1939a, b, 1940a, b, 1942; Ross, 1957, 1971) also present specific differences; in the description of two species of Teratembiidae from Argentina, those characters are used for the first time in females. These characters are also used in the males of the two new species and also in those of *O. unicolor* and *O. bicolor.*

MATERIALS AND METHODS

All measurements are given in millimeters. Ocular ratio is defined as the ratio between minimum distance between inner edges of eyes, and maximum distance of outer edges, in dorsal view.

The material examined is deposited in the Museo Argentino de Ciencias Naturales Bernardino Rivadavia (MACN) and in the Facultad de Ciencias Exactas y Naturales de la Universidad de Buenos Aires (FCEN).

Abbreviations used follow Ross (1944 and subsequent papers): 9T, ninth abdominal tergite; 10T, tenth abdominal tergite; 10L, left hemitergite of tenth abdominal tergite; 10R, right hemitergite of tenth abdominal tergite; MS, medial sclerite of tenth abdominal tergite; 10LP, process of left hemitergite; 10RP, process of right hemitergite; EP, epiproct; LPPT, left paraproct; RPPT, right paraproct; H, hypandrium or ninth abdominal sternite; HP, process of ninth sternite; LCB, left cercus-basipodite; RCB, right cercus-basipodite; LCBP, process of left cercus-basipodite.

Descriptions are based on only one specimen; variation observed on other specimens is pointed out separately, with the mean value followed by standard deviation and range, in parentheses; for proportions, only the range is given.

Setae are omitted in the drawings of terminalia.

Genus *Diradius* Friederichs, 1934

According to Ross (1984b:45) this genus differs from *Oligembia* Davis by the following characters of the male terminalia: 1—“. . . complete absence of fusion lines between 10L, 10R and medial sclerite (MS) . . . .” 2—“. . . outer side of the right hemitergite (10R) . . . at least as long as outer margin of 10L . . . .” 3—“. . . usual presence of lobe beneath the “claw”-bearing lobe of the left cercus-basipodite . . . .”

The only character that really distinguishes *Diradius* from *Oligembia* (and all the embidiina) is the last one, previously mentioned by Ross (1944:476) as “LCB with two inner lobes, the ventral one usually shorter and broadly pointed, the upper lobe enlongate with a terminal cleft forming rather long “claws” which may at times be fused together . . . .”

Species transferred by Ross (1984a:90) to the genus *Diradius* lack the former two characters mentioned. *Diradius lobatus* (Ross, 1944: fig. 128); *Diradius excissa* (Ross, 1944: fig. 139); *Diradius plaumanni* (Ross, 1944: fig. 143); *Diradius vandikei* (Ross, 1944: fig. 152); *Diradius nigrina* (Ross, 1944: fig. 149), have a “fusion line” between 10L and MS. Although *some* species of *Diradius* differ from *Oligembia* in this character, the same is not true for *all* the species in the genus.

The situation is similar with regard to the outer margin of the 10R. *Diradius chiapae* (Ross, 1944: fig. 137), *D. excissa* (Ross, 1944: fig. 140) and *D. nigrina* (Ross, 1944: fig. 150), have the outer margin of the 10R slightly shorter than the outer margin of the 10L, and species as *D. plaumanni* (Ross, 1944: fig. 143), *D. gigantea* (Ross, 1944: fig. 146), *D. vandykei* (Ross, 1944: fig. 152) and *D. caribbeana* (Ross, 1944: fig. 155), have the outer margin of the 10R clearly shorter than that of the 10L.

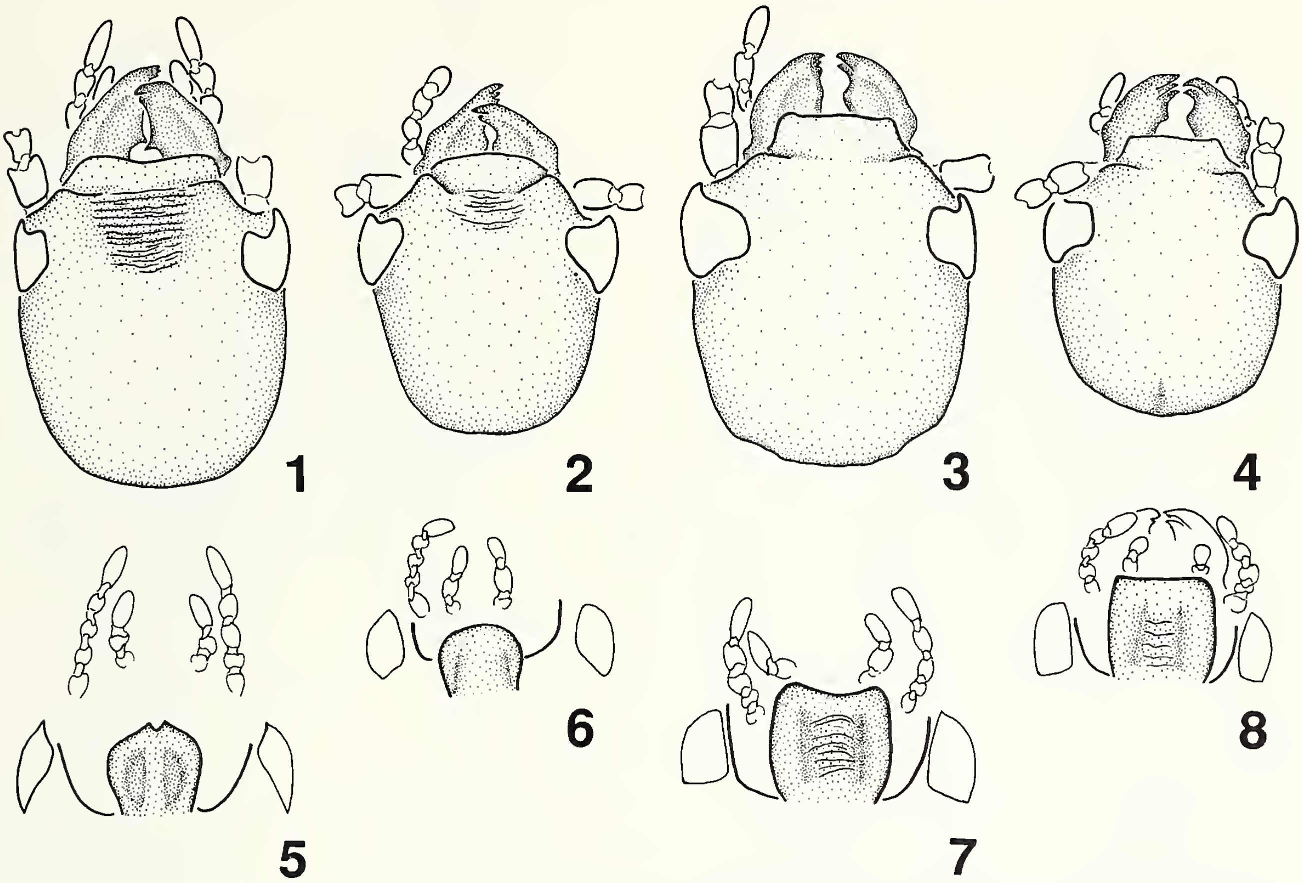
Diradius erba, new species
(Figs. 1, 5, 9, 11, 17, 18, 21, 23, 29)

Diagnosis. Diradius erba is closest to *Oligembia unicolor* Ross, 1944. *Diradius erba* has the apex of LCBP with lateral margins convergent and straight, with two blunt apical spines, the anterior margin of the submentum with two triangular mesial projections, the margin of 10L, 10R and MS with depressions towards the base of 10RP, marked by deep lines. *Oligembia unicolor,* instead, has the apex of LCBP with lateral margins irregular and divergent, forming a circular plate with two projecting spines, the anterior margin of submentum rounded, and the margin of 10L, 10R and MS without depressions.

Types. Holotype male (in alcohol) from Argentina, Entre Rios Prov., Balneario La Lana, 5 6 XII 1987, C. Szumik, P. Goloboff col. (MACN) Paratypes: three males, same data as the holotype (MACN); male and female from Argentina: Buenos Aires Prov., Otamendi, INTA Delta, 14 15 XII 1988, C. Szumik, A. Valverde col. (MACN).

Etymology. The specific name is formed with the initials of the provinces where the species has been collected.

Male holotype. Total length: 4.90. Head (Fig. 1): rectangular, width/length, 0.68. Eyes very small, ocular ratio: 0.74. Mandibles (Fig. 1): left with three very short, inconspicuous teeth in the tip; inner margins with a very sharp and conspicuous basal tooth. Submentum: anterior margin with two short triangular projections and a small notch between them (Fig. 5). Wing lengths: anterior, 3.40; posterior, 2.75. Wing venation similar to the venation illustrated by Mariño and Marquez (1982:



Figs. 1–8. Males. 1–4. Head, dorsal, 5–8. Submentum. 1, 5. *Diradius erba*. 2, 6. *Oligembia unicolor*. 3, 7. *O. mini*. 4, 8. *O. bicolor*.

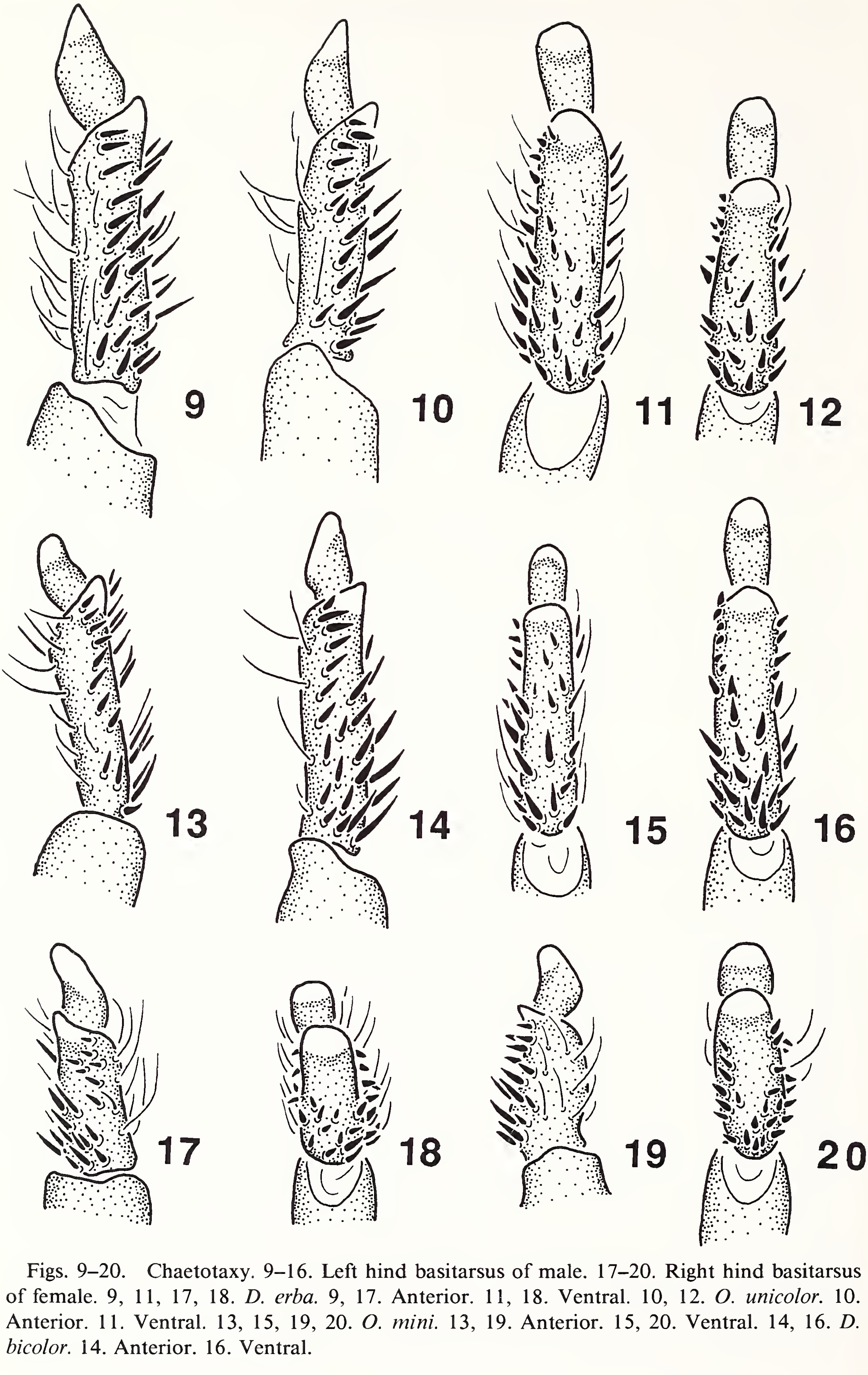
Figs. 12, 13) for *Diradius cristobalensis*: Ma, Ma1, Ma2, Mp, Cua y A inconspicuous, marked by rows of macrotrichia; Ma forked, the rest unforked. Cross veins: anterior wing: 3 or 5 between C and R1, 3 between R1 and Rs; posterior wing: 3 or 5 between C and R1, 4 to 5 between R1 and Rs.

Hind leg: total length, 1.74. Hind basitarsus, length: 0.19, width/length: 0.28; setae as in Figures 9, 11.

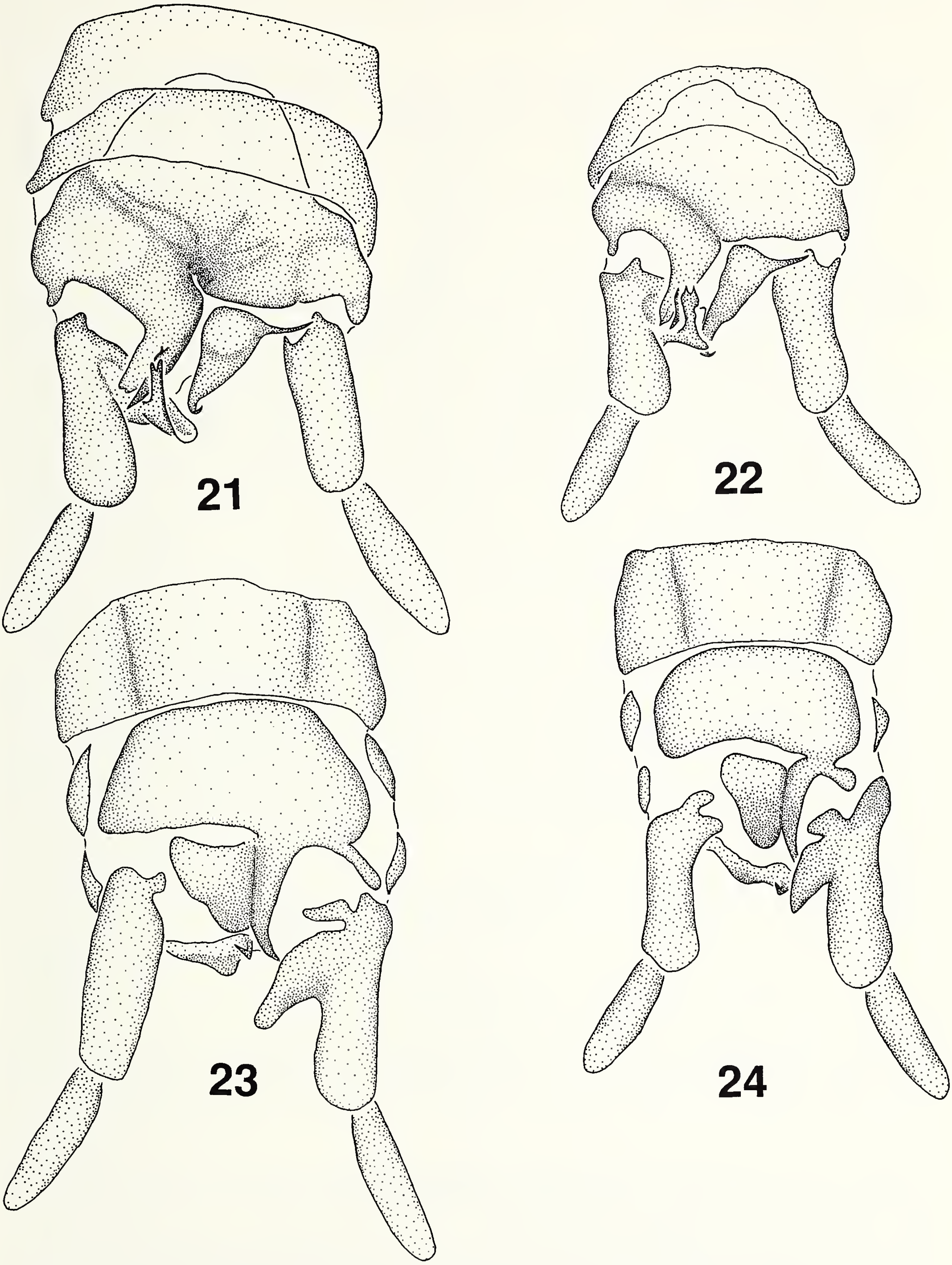
Head black-brown, labrum yellowish white, maxillary and mandibular palpi, mandibles, and eyes brown; 1st and 2nd antennal segments black-brown, 3rd to 5th yellowish, 6th to 8th slightly tan, the rest brown. Thorax brown, joints of sclerites and wings orangish tan. Tarsi of mid and hind legs yellowish, the rest brown. Abdomen: segments 9 and 10 brown, second segment of cerci with yellowish apex, the rest orangish tan.

Terminalia: Figures 21, 23, 29. MS extending to the anterior margin of the 9T. Fusion lines present between MS and 10L, and between MS and 10R, the latter shallow and inconspicuous; MS and 10R depressed towards the base of 10RP, with very conspicuous ridges. LPPT partially fused to the H, with anterior end blunt and posterior end sharp, the latter extending dorsally. LCB differentiated from the rest of the segment by being more pigmented and sclerotized.

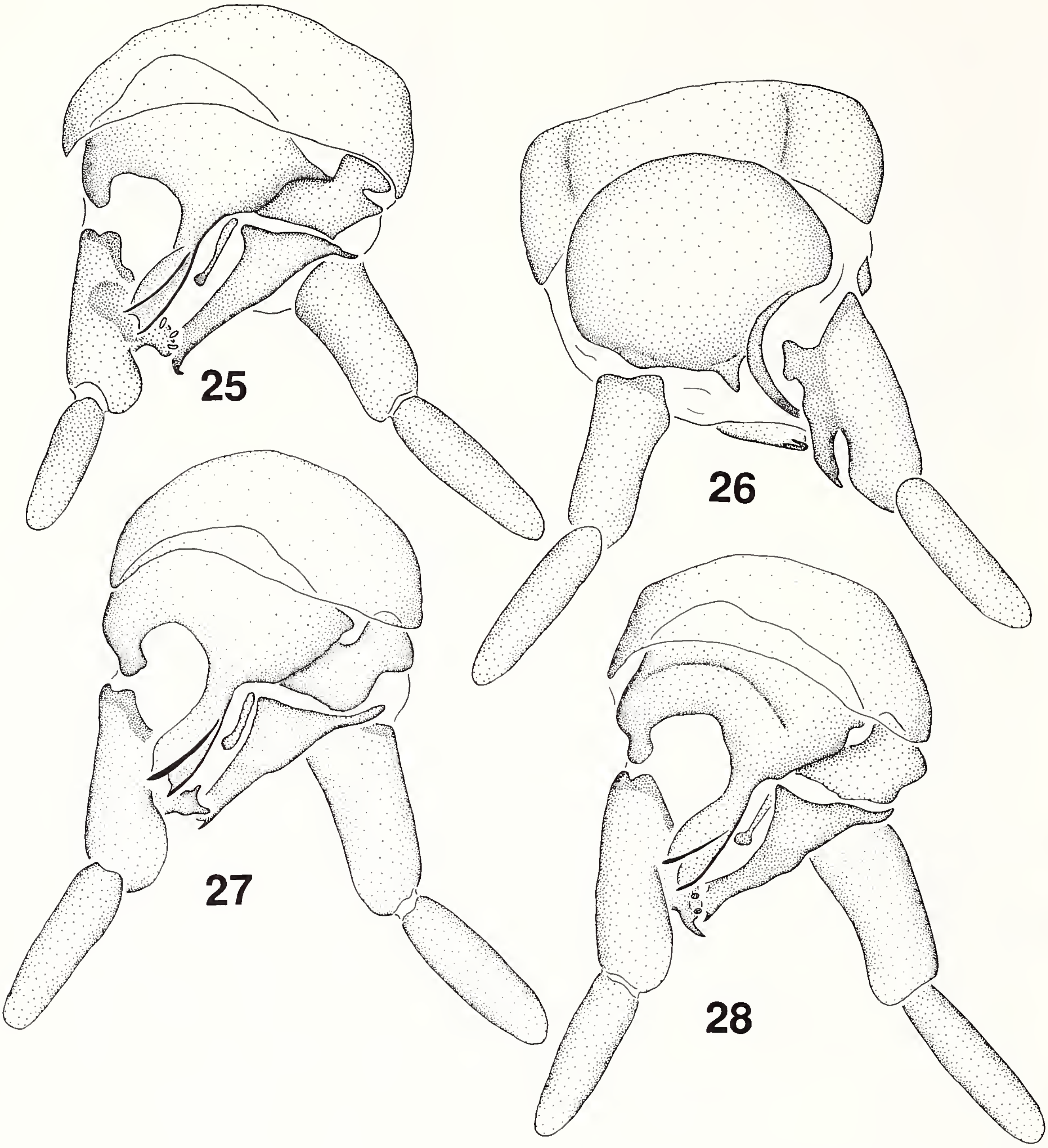
Variation. Total length, 4.51 (±0.37, 4.00–5.00, N = 8). Head, width/length ratio varies between 0.65 and 0.72. Ocular ratio: 0.62–0.74. Wing length: anterior, 3.40 (±0.13, 3.20–3.60); posterior, 2.66 (±0.08, 2.50–2.75). Cross veins: anterior wing, 3 to 9 between C and R1, 2 to 6 between R1 and Rs; posterior wing, 2 to 7 between



Figs. 9–20. Chaetotaxy. 9–16. Left hind basitarsus of male. 17–20. Right hind basitarsus of female. 9, 11, 17, 18. *D. erba*. 9, 17. Anterior. 11, 18. Ventral. 10, 12. *O. unicolor*. 10. Anterior. 11. Ventral. 13, 15, 19, 20. *O. mini*. 13, 19. Anterior. 15, 20. Ventral. 14, 16. *D. bicolor*. 14. Anterior. 16. Ventral.



Figs. 21–24. Terminalia of male. 21, 22. Dorsal. 23, 24. Ventral. 21, 23. *D. erba*. 22, 24. *O. unicolor*.



Figs. 25–28. Terminalia of male. 25, 27, 28. Dorsal. 26. Ventral. 25, 26. *O. mini.* 27, 28. *O. bicolor.*

C and R1, 3 to 5 between R1 and Rs. Rs of left anterior wing is forked in one of the paratypes from the topotypic locality.

Posterior leg: total length, 1.73 (±0.08, 1.60–1.91); basitarsus, length: 0.20 (±0.01, 0.19–0.23), width/length: 0.24–0.32.

A male from Chascomús has the 1st and 2nd antennal segments black-brown, 3rd to 6th yellowish, the rest brown.

Female paratype. Total length: 4.45. Head: width/length, 0.79. Ocular ratio: 0.82. Hind leg: total length, 1.50; basitarsus, length: 0.13, width/length: 0.49. Hind basitarsus: anterior face, apical half with 4 to 6 short macrosetae directed toward the

base of the article (Fig. 17); ventral face with macrosetae only on its basal half (Fig. 18).

Head, maxillary and mandibular palpi, mandibles and antennae brown. Prothorax and mesothorax brown, metathorax tan. Legs: mid and hind tarsi slightly tan, the rest brown. Abdomen: 8th, 9th and 10th segments and basal segment of cercus brown, the rest tan.

Variation. No significant differences were observed in the only other adult female examined.

Biology. The specimens were collected on "Espinillo" (*Acacia caven,* Leguminosae) and *Eucalyptus* sp. The nests were found under bark, with very short portions of the galleries uncovered. Four nests were observed, one with an adult female, another with an adult male, and two with groups of juveniles.

Discussion. Additional differences with *Oligembia unicolor* (observations made on a male from the topotypic locality, Nova Teutonia, Brazil, Ross col., E. S. Ross det. 1990) are: left mandible with three short and conspicuous teeth (Fig. 2); inner basal margins of both mandibles with rounded (instead of sharp) teeth (Fig. 2); submentum: anterior margin convex (Fig. 6); outer and inner processes of 10LP of the same length; 10T reaching the middle of 9T (Fig. 22); anterior margin of LPP fused only a short distance to the H; anterior edge of LPP rounded, posterior tip sharp; H rectangular (Fig. 24). With regard to the hind basitarsus chaetotaxy (Figs. 10, 12), no significant differences with *D. erba* were observed.

Some of the characters mentioned above do not coincided with the description of the holotype of *Oligembia unicolor* by Ross (1944:471, figs. 115–117). The H is described there as having "each corner produced as a narrow, truncate projection." The LCBP is described (p. 470) as an ". . . inner projection sclerotic, with a dorsal pair of short serrations . . ." (in the topotype the LCBP (see Figs. 22, 30) arises ventrally and laterally, shaped as a lamina, and subapically on this a second process—mentioned above—is set).

It seems evident, on the light of the above comments, that *O. unicolor* belongs to *Diradius.* However, no new combination is formally proposed here, on the assumption that E. S. Ross in his intended revision of the Embiidina, will discuss the systematic position of this species.

Distribution. Argentina: Provinces of Buenos Aires and Entre Rios.

Other material examined. Argentina: Entre Rios prov.: El Palmar, 11 IX 1985, Maloné col., male (FCEN); Balneario La Lana, 5 6 XII 1987, C. Szumik, P. Goloboff col., 2 juvenile males (MACN); Buenos Aires prov.: Otamendi, INTA Delta, 2 VII 1969, male (FCEN); Chascomús, V 1989, S. Mazzucconi col., male and female (MACN).

Genus *Oligembia* Davis, 1939

According to Ross (1984b:43) the males of *Oligembia* Davis would differ from those of *Diradius* Friederichs by the following characters of the terminalia: 1—". . . lines of fusion of 10L, 10R and MS still evident as shallow indistinct grooves . . ."; 2—"10R with outer side short . . .(in . . ."; 3—"10LP with inner and outer processes subequal," and 4—"LCB has only a single inner process terminated by minute bifurcation."

Contrary to Ross' statements, the only character that distinguishes all species of

this genus from *Diradius* (and other Teratembiidae) is the 10LP with subequal inner and outer portions. However, this is a plesiomorphic state and no apomorphy supporting the monophyly of *Oligembia* is known. The other characters that Ross mentions for *Oligembia* are also found in some species of Teratembiidae that do not belong to *Oligembia* (for example see comments under *Diradius*; these characters thus appear to be apomorphies at higher levels than this genus.

Oligembia mini, new species
(Figs. 3, 7, 13, 15, 19, 20, 25, 26, 31)

Diagnosis. O. mini is closest to *O. bicolor* Ross, 1944, but it can be distinguished by having the apex of the LCBP with three sharp apical points instead of two (a third point found in some males of *O. bicolor* is situated in the middle of the process).

Types. Holotype male (in alcohol, terminalia treated with alcali) from Argentina, Misiones Prov., Parque Nacional Iguazú, area cataratas, 31 I 1988, C. Szumik, P. Goloboff col. (MACN); Paratypes: male (hind pair of legs missing, wings in bad condition) and female, with same data as the holotype (MACN).

Etymology. The specific name refers to the size of the specimens (from the guaraní, miní = small).

Male holotype. Total length: 3.95. Head (Fig. 3): width/length, 0.73; Mandible: with very short teeth (Fig. 3); Submentum: anterior margin strongly concave (Fig. 7). Eyes quadrangular, ocular ratio: 0.65. Wing length: anterior, 2.85; posterior, 2.05. Wing venation similar to the venation illustrated by Davis (1939a: Fig. 2) for *Oligembia hubbardi*: R1, Cu1b and A conspicuous, the rest marked by rows of macrotrichia; Ma forked, the rest unforked; cross veins: anterior wing: 4 or 6 between C and R1, 2 between R1 and Rs; posterior wing: 5 between C and R1, 4 between R1 and Rs.

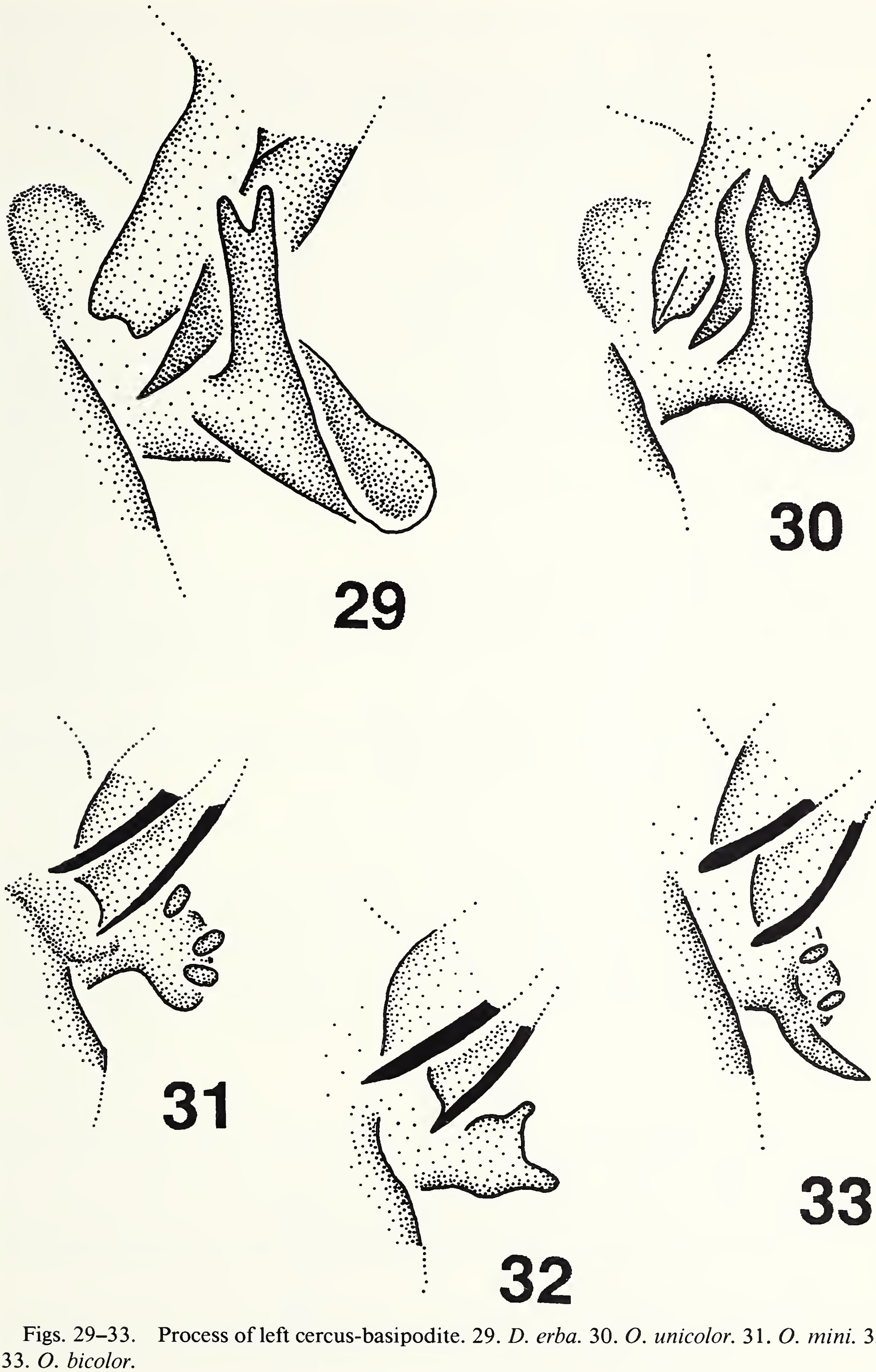
Hind leg: total length, 1.59. Hind basitarsus, length: 0.20, width/length: 0.25, disposition of setae in Figures 13, 15.

Head brown, labrum, maxillary and mandibular palpi and eyes slightly tan; antennae: 2nd segment yellowish, the rest slightly tan. Prothorax yellowish, mesothorax and metathorax slightly tan. Legs: coxa and trochanter of the three pairs and tibia and tarsus of the mid pair yellowish, the rest brown. Abdomen: 10th segment brown, and apex of 2nd segment of the cerci yellowish; the rest slightly tan.

Terminalia: Figures 25, 26, 31. 10R separated from MS by irregular membranous band. 10R with irregular margin, not extended towards the 9T. Apex of 10RP extended towards the right side. Posterior margin of the 10L slightly curved toward anterior margin; fusion line present between 10L and MS. H semicircular; HP triangular without transverse lines. LCBP with base ventral and inner, extended dorsally, with three sharp points in the apex, no more sclerotized than the rest of the LCBP.

Female paratype. Total length: 4.65. Head: width/length, 0.77. Ocular ratio: 0.83. Hind legs: total length, 1.21; hind basitarsus, length: 0.13, width/length: 0.45. Setae as in Figures 19–20.

Head orangish tan, eyes black, labrum yellow white, maxillary and mandibular palpi and 11th basal antennal segments slightly tan, 12th antennal segment yellow white. Prothorax and joints between thoracic sclerites yellow white, mesothorax and metathorax slightly tan. Legs: coxa and trochanter of the three pairs, and tibia and



Figs. 29–33. Process of left cercus-basipodite. 29. *D. erba*. 30. *O. unicolor*. 31. *O. mini*. 32, 33. *O. bicolor*.

tarsus of the hind pair yellow white, the rest slightly tan. Abdomen slightly tan, joints among segments yellow white; 1st segment of cercus yellow white, 2nd segment yellowish white. Apical segment of the cercus short and conical.

Variation. Aside from the specimens described, only one adult male and one adult female were examined; no significant variation was observed on these specimens.

Biology. The specimens were collected in nests between mosses growing on stones and roots of the banks of the Iguazú river; the tubes deepened 1 to 2 cm beneath the surface. The environment was very humid. Two nests were observed; both with an adult female and juveniles, one also with an adult male. The other male examined was collected as a juvenile and matured in captivity (in February).

Discussion. Four topotypic males of *Oligembia bicolor* (from Brazil, Nova Teutonia, matured 31 III 1965, Ross. col., E. S. Ross det. 1990) show the following additional differences with *O. mini*: apical mandibular teeth conspicuous (Fig. 4); anterior margin of the submentum slightly concave (Fig. 8); 10R with a more regular margin, apex of 10RP extended towards the left (Figs. 27, 28); HP with many transverse lines; LCBP (Figs. 28, 33) with two points in the apex, and another one in the middle of the process (one of the four specimens, Figures 27 and 32, lacks the latter point).

No significant differences with *O. mini* were observed in the disposition of setae in the hind basitarsus of *O. bicolor* (Figs. 14–16).

In the original description of *O. bicolor* (Ross, 1944:469, Figs. 108–110) the LCBP is described as a "conical lobe with two projections," and the third projection in the middle of the process (observed in three of the four topotypic specimens) is not mentioned.

Distribution. Known only from the type locality.

Other material examined. One adult female, six juvenile females and seven juvenile males, with same data as the holotype (MACN).

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EGG ULTRASTRUCTURE AND DESCRIPTIONS OF NYMPHS OF *PELOCORIS POEYI* (GUÉRIN MÉNEVILLE) (HEMIPTERA: NAUCORIDAE)

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Abstract.—Adults and first through fifth instars of *Pelocoris poeyi* were collected from two localities in Amazonian Ecuador. Immatures occurred syntopically with adults and were found among vegetation in standing water. The existence of five nymphal instars was confirmed with Discriminant Function Analysis based on a suite of external mensural characters. Eggs have two partially fused, coiled micropyles at the anterior pole. First instars are impunctate, whereas the remaining instars are punctate in discrete patterns. Second through fifth instars are separable based on relative length of the mesonotal wingpad compared with the exposed part of the metanotal lateral margin. Scanning electron micrographs of eggs are presented and all immature stages described and illustrated.

The genus *Pelocoris* (Hemiptera: Naucoridae) is restricted to the New World and comprises 17 species (La Rivers, 1971, 1974, 1976). Of these, the immature stages have been described for only *P. f. femoratus* Palisot de Beauvois (Torre Bueno, 1903; Hungerford, 1920; McPherson et al., 1987). *Pelocoris poeyi* (Guérin Méneville) was described in 1835 via an iconograph; the accompanying text was published in 1844. More recently, Nieser (1975) provided a comparative description of *P. poeyi* and with it synonymized *P. convexus* Nieser.

The currently known range of *P. poeyi* is throughout much of the Caribbean Islands and tropical South America. It has been reported specifically from Aruba, Barbuda, Curaçao, Guadeloupe, Iles-des-Saintes, Marie-Galante, Puerto Rico, St. Croix, and Trinidad (Nieser, 1969), Brazil, Guyana, and Suriname (Nieser, 1975), Cuba (Nieser, 1977), and Ecuador (Sites, 1990). Only several ecological notes have been published for *P. poeyi*; Nieser (1975) reported that in Suriname it occurs in saline water and is abundant in stagnant water with aquatic vegetation. Sites (1990) reported that in Ecuador, *P. poeyi* occurs with other aquatic Hemiptera, including *Belostoma plebejum* (Stål) (Belostomatidae), *Heterocorixa w. wrighti* Hungerford (Corixidae), and *Notonecta pulchra* Hungerford (Notonectidae), and that nymphs are syntopic with adults in springs and swamps. Scanning electron micrographs of egg ultrastructure and descriptions of all immature stages of *P. poeyi* from Ecuador are presented herein.

MATERIALS AND METHODS

Adults and first through fifth instars of *P. poeyi* were collected from two localities in Napo Province, Ecuador [see Sites (1990) for precise localities and descriptions of habitats]. Submergent and emergent vegetation in swampy situations and a spring fed pool were swept with an aquatic D-net; adults and all nymphal stages were collected from the same habitats. All specimens were fixed in 70% isopropyl alcohol for ca. 2 weeks, then preserved in 70% ethyl alcohol. Voucher specimens are housed

in the Enns Entomological Collection, University of Missouri. Eggs were obtained by dissecting females preserved in alcohol. Only eggs contained in the common oviduct or vagina were used for scanning electron microscopy and measurements. All measurements are based on 10 individuals of each stage. Linear measurements [mm ($\bar{y}$ ± SE)] were made with an ocular micrometer.

DESCRIPTIONS OF IMMATURES

Egg (Fig. 1). Length, 1.38 ± 0.01 mm; width, 0.67 ± 0.01 mm. Egg elongate and slightly reniform with rounded ends (Fig. 1A); color creamy white; polygonal reticulation pattern on surface generally pentagonal or hexagonal (Fig. 1B); reticulation composed of a series of depressed lines; each polygon with 10–20 slightly-domed pore canals within (Fig. 1C); anterior pole with micropyles situated among polygons with raised ridges, with pore canals poorly developed or absent (Fig. 1D); two partially fused, coiled micropyles at anterior pole (Fig. 1E); micropyles arising from single, twisted stalk (Fig. 1F).

Nymphs. The only congener of *P. poeyi* for which the instar number is known is *P. femoratus* Palisot de Beauvois with five nymphal instars (Torre Bueno, 1903). Under the presumption that *P. poeyi* also has five instars, Discriminant Function Analysis (DFA) was performed on the raw data summarized in Table 1 to determine if these data completely separate into five groups. The DFA was significant (χ^2 = 396.8, df = 72, $P \ll 0.001$) and the corresponding classification phase of DFA correctly assigned 100% of the cases to the appropriate instar. Thus, even without data on rearing, *P. poeyi* also appears to have five instars.

The first instar is described in detail and only changes in subsequent instars are described. Patterns and extent of maculation are variable among individuals. Length is measured from tip of tylus to tip of abdomen; width is measured across metathorax. Because individual naucorid size varies with environmental temperature during development (see Sites & Nichols, 1990), the mean body/head dorsal surface area ratio is given for each instar as measure of allometric growth, and was calculated using a digitizer (Macintizer, GTCO Corp.) and camera lucida. The digitized ratios and additional measurements are given in Table 1.

First instar (Fig. 2A). Body elongate, parallel-sided, greatest width at metathorax; general appearance dorsally and ventromedially convex, ventrolaterally concave; posterior end slightly produced to a point; dorsally dark brown with yellowish brown areas, ventrally yellowish brown.

Head broadly triangular; anterior margin convex, continuous with lateral margins of prothorax; posterior margin lobate and deeply convex medially. Head dark brown with yellowish brown areas along mesal margins of compound eyes dorsally; yellowish brown ventrally. Compound eye red, synthlipsis (measured at anterior margin of eyes) ca. 3.5 × width of one eye. Antenna three-segmented, segment one yellowish brown, segments two and three dark brown; segment two ca. 2.0 × length of segment one and ca. 0.7 × length of segment three. Beak dark brown, elongate-conical, three-segmented with segment one concealed beneath labrum, overall length ca. 1.4 × width at base, segment two ca. 3.0 × length of segment one and 1.2 × length of segment three.

Nota dark brown with yellowish brown areas behind compound eyes and at pos-

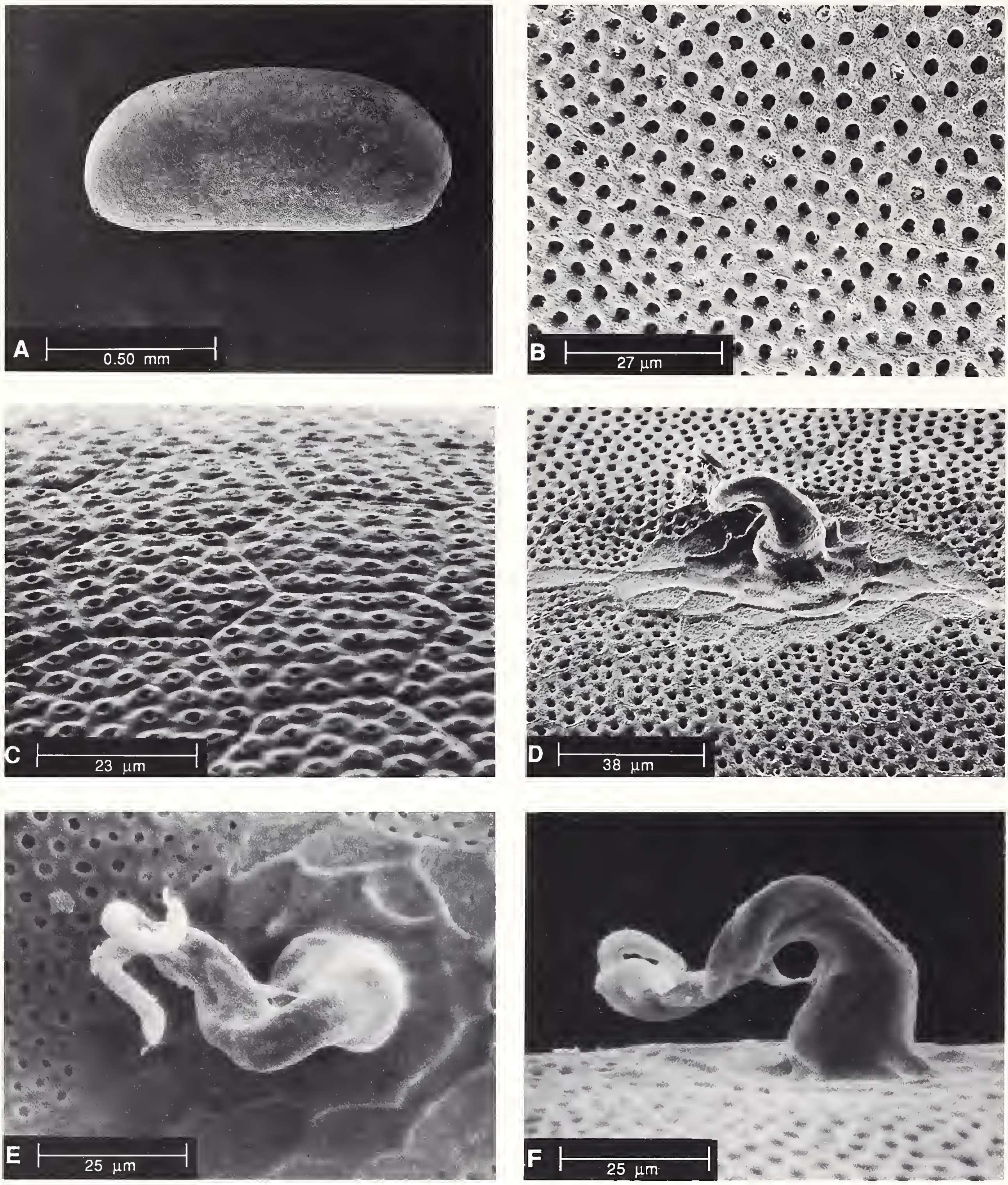

Fig. 1. Scanning electron micrographs of *Pelocoris poeyi.* A. Intact egg. B. Polygonal reticulation pattern of chorion and pore canals. C. Domed pore canals and depressed lines forming reticulation. D. Anterior pole with micropyles and modified chorionic sculpturing. E. Paired, coiled micropyles (end view). F. Micropyles arising from single, twisted stalk (lateral view).

terolateral corners of each notum; mid-dorsal longitudinal suture from anterior margin of pronotum to ¾ length of metanotum. Pronotum with anterior margin lobate and deeply concave medially to abut posterior margin of head; posterior margin nearly straight; pronotum overlaps 20–40% of mesonotum. Mesonotum shortest of nota, ca. 0.9 × length of pronotum at midline; posterior margin convex laterally and

Table 1. Descriptive measurements (mm)[a] and body/head ratios of *Pelocoris poeyi* instars.

Character[b]	Nymph				
	1st instar	2nd instar	3rd instar	4th instar	5th instar
Body/head area[c]	7.19 ± 0.14	8.66 ± 0.29	10.28 ± 0.21	12.03 ± 0.34	12.64 ± 0.22
Body length	2.26 ± 0.02	3.01 ± 0.02	4.16 ± 0.06	5.55 ± 0.05	7.55 ± 0.13
Body width	1.43 ± 0.02	1.99 ± 0.01	2.75 ± 0.03	3.70 ± 0.04	5.03 ± 0.08
Head length	0.64 ± 0.01	0.80 ± 0.01	1.02 ± 0.02	1.26 ± 0.01	1.53 ± 0.03
Head width	0.86 ± 0.02	1.16 ± 0.01	1.55 ± 0.01	2.01 ± 0.02	2.64 ± 0.04
Synthlipsis	0.42 ± 0.01	0.54 ± 0.01	0.67 ± 0.01	0.80 ± 0.02	0.96 ± 0.04
Pronotal length	0.23 ± 0.00	0.40 ± 0.00	0.60 ± 0.01	0.89 ± 0.01	1.33 ± 0.02
Mesonotal length	0.20 ± 0.01	0.37 ± 0.01	0.56 ± 0.01	0.84 ± 0.02	1.23 ± 0.03
Metanotal length	0.29 ± 0.01	0.40 ± 0.00	0.56 ± 0.01	0.70 ± 0.01	0.96 ± 0.02
Leg lengths:					
Profemur	0.58 ± 0.01	0.75 ± 0.00	1.02 ± 0.01	1.33 ± 0.01	1.80 ± 0.04
Protibia	0.36 ± 0.01	0.48 ± 0.00	0.68 ± 0.01	0.90 ± 0.01	1.27 ± 0.03
Protarsus	0.21 ± 0.00	0.24 ± 0.00	0.28 ± 0.00	0.30 ± 0.01	0.36 ± 0.01
Mesofemur	0.50 ± 0.00	0.68 ± 0.00	0.89 ± 0.01	1.20 ± 0.01	1.63 ± 0.04
Mesotibia	0.39 ± 0.00	0.51 ± 0.01	0.69 ± 0.01	0.92 ± 0.01	1.26 ± 0.04
Mesotarsus	0.24 ± 0.00	0.29 ± 0.00	0.36 ± 0.00	0.46 ± 0.01	0.59 ± 0.01
Metafemur	0.62 ± 0.00	0.87 ± 0.00	1.17 ± 0.02	1.56 ± 0.01	2.12 ± 0.04
Metatibia	0.64 ± 0.01	0.87 ± 0.00	1.18 ± 0.02	1.55 ± 0.01	2.13 ± 0.06
Metatarsus	0.36 ± 0.01	0.45 ± 0.00	0.57 ± 0.01	0.72 ± 0.01	0.96 ± 0.02

[a] $\bar{y} \pm$ SE; SE values less than 0.005 are listed as 0.00; measurements are based on 10 individuals.
[b] Synthlipsis measured at anterior margin, leg segments at longest points, other lengths at midline, widths at greatest distance.
[c] Ratio is mean body/head dorsal surface area and was calculated using digitized areas.

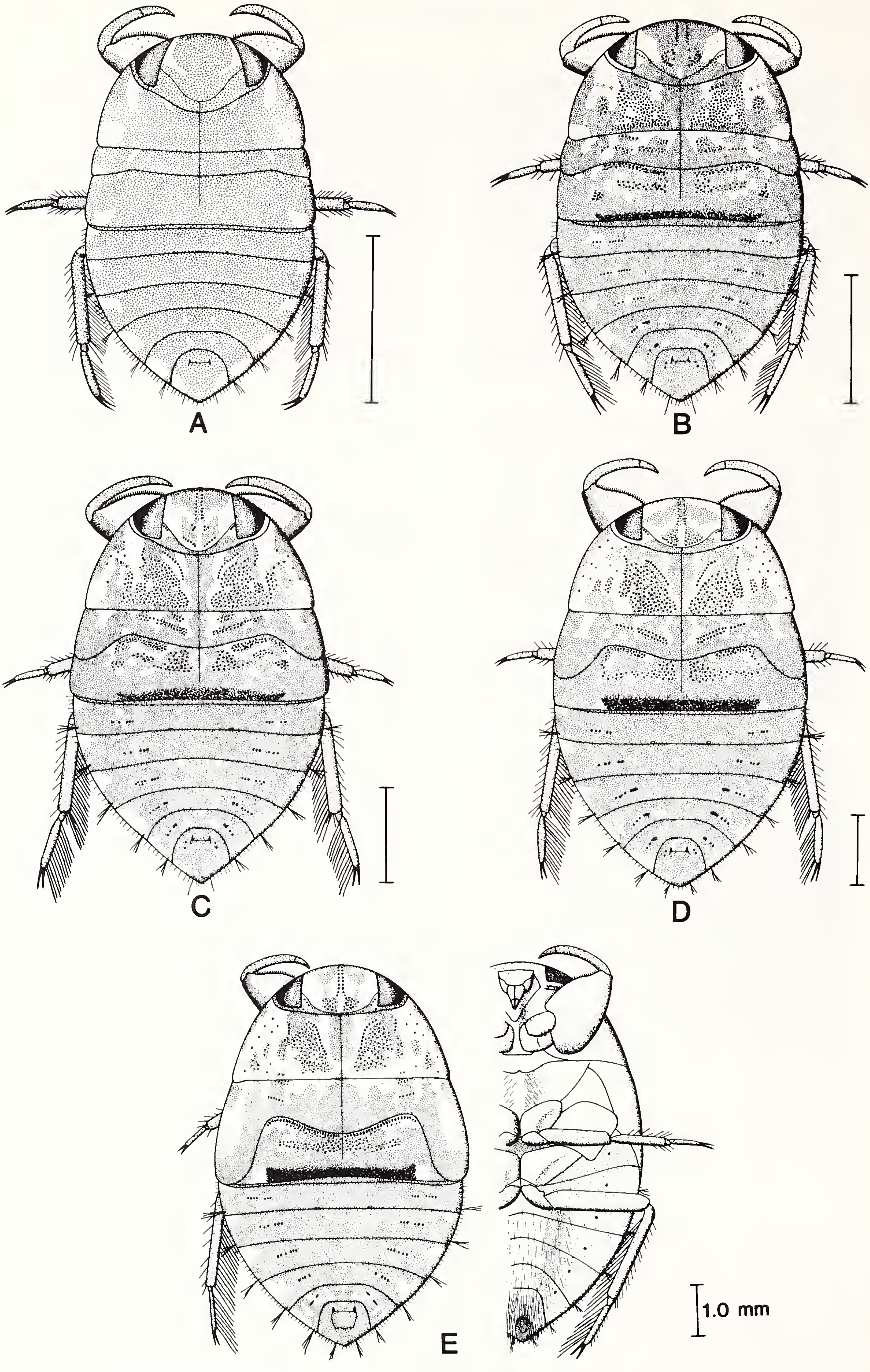

Fig. 2. Nymphal instars of *Pelocoris poeyi.* A. First instar. B. Second instar. C. Third instar. D. Fourth instar. E. Fifth instar.

slightly convex medially. Metanotum longest of nota, ca. 1.4 × length of mesonotum at midline; posterior margin shallowly inverted-V shaped. Mesonotal wing pads evident, metanotal wing pads absent. Metanotum completely overlaps abdominal tergum I and 70–90% of tergum II.

Prothoracic leg retentorial (see Sites and Nichols, 1990); tibia and tarsus dark brown and femur light brown with dark brown dorsal margin, trochanter dark brown ventrally, and coxa light brown. Procoxa ca. 1.9 × length of trochanter and ca. 0.7 × length of femur. Profemur laterally compressed; two rows of pegs directed ventrolaterally and ventromedially with row of slender setae between, pegs gradually shortening distally so that distal pegs are 0.5–0.2 × length of basal pegs; row of stout setae at base on lateral surface. Protibia and protarsus with sulcus extending length of ventral surface, sulcus with row of spatulate setae from near base of tibia to basal ⅓ of tarsus; femoral pegs embrace sides of tibia and tarsus when appressed; tarsus one-segmented with a single terminal claw.

Meso- and metathoracic legs dark brown; all segments of metathoracic leg longer than corresponding segments of mesothoracic leg. Mesocoxa conical, ca. 2 × length of semicircular trochanter and 0.7 × length of femur. Meso- and metacoxa with 2–3 short spines along ventral ridge. Mesofemur with 3 rows of pegs: 3–5 posteroventral, 9–11 posterodorsal, and 9–11 recurved pegs on anterior margin; anterior and posteroventral peg numbers exclude contiguous apical groups; pegs on posteroventral and anterior margins gradually lengthening distally so that distal pegs are spine-like; mesofemur with row of 4 stout setae at posteroventral apex and 2 at anteroventral apex; mesofemur ca. 1.2 × length of mesotibia. Mesotibia with four rows of stout spines (two ventral, one anterior, one posterior). Mesotarsus two-segmented, first segment 0.3 × length of second and lobed ¾ its length under second, second segment with two rows of spines. Claws paired and equal, 0.4 × length of tarsus. Metacoxa and trochanter resembling those of mesothoracic leg in shape and proportions. Metafemur with 4 rows of pegs: 14–16 posteroventral, 7–9 posterodorsal paralleled by a row of smaller pegs that curve anteriorly near junction with trochanter, 11–13 anterior; anterior and posteroventral peg numbers exclude contiguous apical groups; metafemur subequal in length to metatibia. Metatarsus with first segment ca. 0.2 × length of second, second segment with two rows of spines. Natatorial hairs sparse on mesotibia and tarsus, abundant on metatibia and tarsus.

Abdomen dorsally dark brown with yellowish brown area at anterolateral corner of each tergum and on each side of the midline of terga III–VII (the latter are more strongly developed posteriorly, and tend to become reduced or absent anteriorly); ventrally yellowish brown with dark brown sternum IX; lateral margins of segments III–VIII finely serrate; ventrally finely setose with middle ⅓ convex and covered with long setae, glabrous band on lateral $\frac{1}{10}$ of each sternum; spiracles present ¼ distance from lateral margin to midline on segments I–VIII, those on segment I concealed in posterolateral corner of the metacoxal cavity; spiracles on segment I elongate-oval, those on segments II–VIII circular. Paired ostioles of scent glands dorsally at posterior margin of tergum III. Two transverse, paired series of punctures on each of terga III–VII.

Second instar (Fig. 2B). Coloration lighter, more distinctly patterned with brown and yellowish brown. Dorsal punctation in distinct patterns. Posterior margin of head less deeply lobed into anterior margin of pronotum. Antenna with segment two ca.

2.5 × length of segment one and ca. 0.6 × length of segment three. Nota brown with yellowish brown mottled pattern; punctation dark brown; dark brown transverse stripe where posterior ⅓ of metanotum overlaps abdominal tergum II. Lengths of pronotum and metanotum subequal at midline and 1.1 × length of mesonotum. Profemur with dense setation ventrally; only one row of pegs. Mesofemur peg numbers: 2–4 posteroventral, 13–17 posterodorsal, 8–10 recurved pegs on anterior margin; mesofemur with row of 7 stout setae at posteroventral apex and 6 at anteroventral apex. Mesotibia with posteroventral row of spines alternately a single large spine with doubled smaller spines; apically with two rows of 4 stout spines ventrally. Metafemur peg numbers: 18–20 posteroventral, 9–11 posterodorsal, 12–14 anterior. Metatibia with two rows of 4 stout spines ventrally. Abdomen with paired series of dark brown punctures ⅓–½ distance from lateral margin to midline on terga III–VII. Sterna V–VIII brown with yellowish brown areas at anterolateral corners and on each side of midline at posterior margins.

Third instar (Fig. 2C). Body shape ovate. Head with posterior margin less deeply lobate into anterior margin of pronotum; color yellowish brown with brown along posterior margin and in anchor shape at midline; brown coloration coincident with punctation. Antenna with segment two ca. 3.0 × length of segment one and ca. 0.6 × length of segment three. Pro-, meso-, and metanotum subequal in length at midline. Mesonotal wing pad length ca. 0.7 × length of exposed part of lateral margin of metanotum. Mesofemur peg numbers: 5–7 posteroventral, 20–22 posterodorsal, 14–16 recurved pegs on anterior margin; mesofemur with row of 9 stout setae at posteroventral apex and 7 at anteroventral apex. Mesotibia with doubled posteroventral spines occasionally tripled; apically with rows of 4 and 5 stout spines ventrally. Metafemur peg numbers: 30–35 posteroventral, 18–21 posterodorsal, 15–18 anterior. Metatibia with two rows of 5 stout spines ventrally. Abdominal terga with yellowish brown areas more pronounced and at the anterior midline and laterally near each punctation series; sterna with conspicuous darkening along midline.

Fourth instar (Fig. 2D). Antenna with segment two ca. 3.5 × length of segment one and ca. 0.5 × length of segment three. Pronotum length subequal to that of mesonotum along midline, and ca. 1.2 × that of metanotum. Profemur with fewer than 10 basal pegs on ventral margin; usually punctate on lateral surface. Mesonotal wing pad length subequal to that of exposed part of lateral margin of metanotum. Mesofemur peg numbers: 7 pegs posteroventral, 28 posterodorsal, 13–15 recurved pegs on anterior margin; mesofemur with row of 12 stout setae at posteroventral apex and 9 at anteroventral apex. Metafemur peg numbers: 40–45 posteroventral, 45–48 posterodorsal, 25–28 anterior. Metatibia with two rows of 6 stout spines ventrally.

Fifth instar (Fig. 2E). Antenna with segment two ca. 3.0 × length of segment one and ca. 0.5 × length of segment three. Mesonotum 0.9 × length of pronotum and 1.3 × that of metanotum at midline. Mesonotal wing pad completely overlaps lateral margin of metanotum and often anterolateral corners of abdominal terga II and III. Mesofemur peg numbers: 8–10 posteroventral, 48–55 posterodorsal, 18–22 recurved pegs along anterior margin; mesofemur with row of 10 stout setae at posteroventral apex and 9 at anteroventral apex. Mesotibia with posteroventral spines alternately one large with tripled or quadrupled smaller spines; apically with rows of 6 and 7

stout spines ventrally. Metafemur peg numbers: 49–52 posteroventral, 44–48 posterodorsal, 26–27 anterior. Metatibia with two rows of 7 stout spines ventrally.

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FOUR NEW SPECIES OF THE NEOTROPICAL GENUS *THERANEIS* SPINOLA (HEMIPTERA: HETEROPTERA: LARGIDAE)

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Abstract.—Four new species of *Theraneis* Spinola, collected in Venezuela, Brazil and Peru are described and illustrated. *Theraneis* is reported for the first time from Venezuela. The distribution pattern of the silvery pubescence as well as the color of the hemelytra are shown to be good characters to distinguish the species. A key for the separation of most of the species is included.

In the general catalogue of the Hemiptera, Fascicle III (Pyrrhocoridae) Hussey and Sherman (1929) recognized ten species within *Theraneis* Spinola (*T. amabilis* Breddin, *T. constricta* Stål, *T. dissimilis* Distant, *T. ferruginea* Mayr, *T. isobel* Hussey, *T. lurida* Distant, *T. oleosa* Distant, *T. pulchra* Distant, *T. spinosa* Distant and *T. vittata* Spinola). Schmidt (1931) described *T. vaga* from Brazil, *T. montivaga* and *T. amabilis* var. *taeniata* from Colombia, and gave new localities for *T. amabilis, T. constricta* and *T. pulchra.* In a recent paper Van Doesburg (1966) described *T. surinamensis* from Suriname.

The type material of the following species was examined; the codens for specimen depositories is given parenthetically: *T. dissimilis* (BMNH), *T. lurida* (BMNH), *T. montivaga* (DEI), *T. oleosa* (BMNH), *T. pulchra* (BMNH), *T. spinosa* (BMNH), *T. surinamensis* (RNHL) and *T. vaga* (DEI). Three species: *T. constricta, T. ferruginea* and *T. isobel* were not located and therefore not examined. In each case only the original description was consulted.

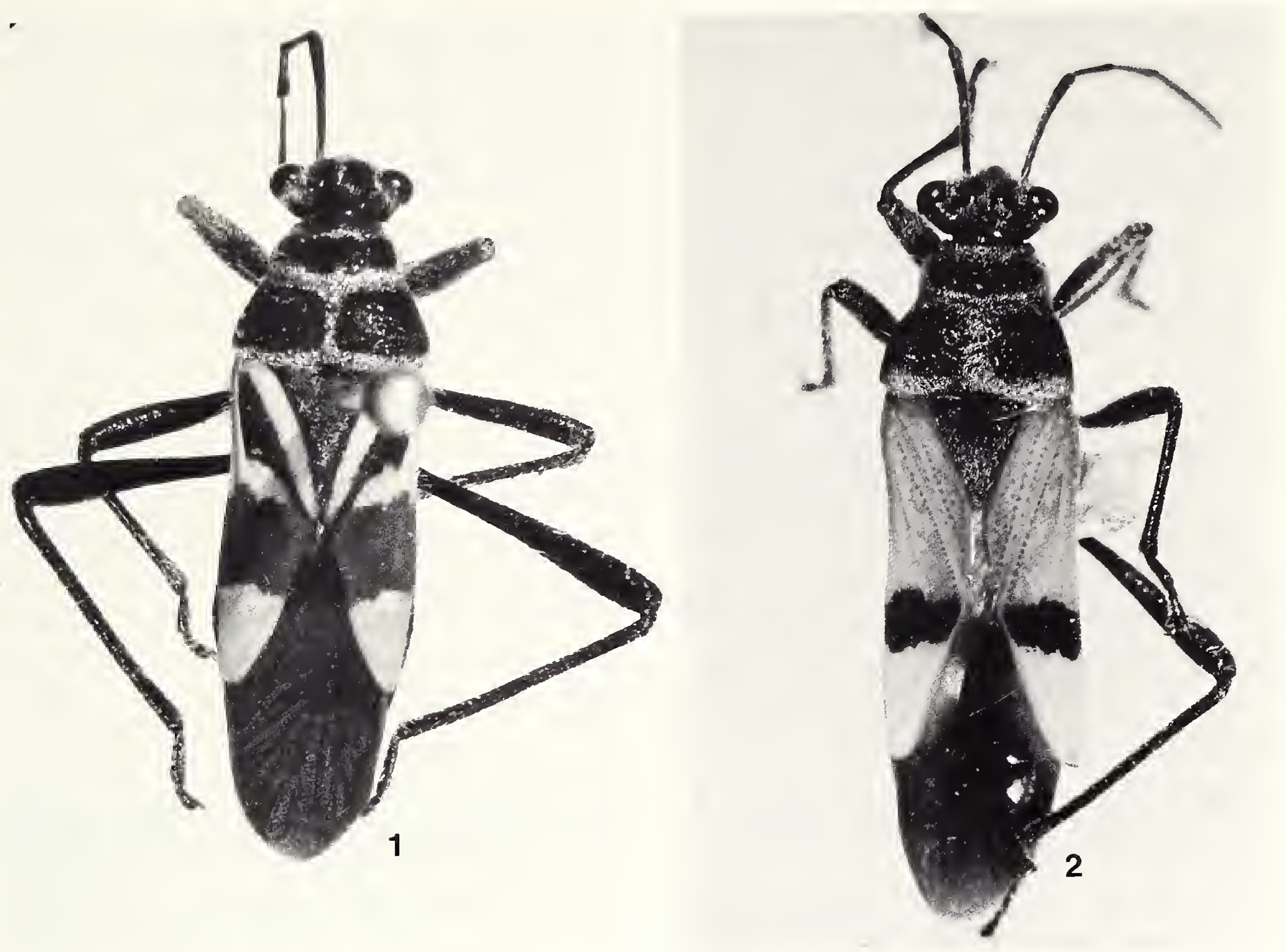
Based on specimens recently examined by the author, four new species are described, therefore *Theraneis* consists of 17 known species and one variety.

The following abbreviations are used in the text: British Museum (Natural History), England. (BMNH); Deutsches Entomologisches Institut, Germany (DEI); Instituto de Biología de la Universidad Nacional Autónoma de México (IBUNAM); Muséum National d'Histoire Naturelle, Paris, France (MNP); Rijksmuseum Van Naturlijke Histoire, Leiden, Netherlands (RNHL); Universidad Central de Venezuela, Escuela de Agronomía, Maracay (UCV); United States National Museum, Smithsonian Institution, Washington, D.C. (USNM).

All measurements are in millimeters.

Theraneis neotropicalis, new species
(Fig. 1)

Female. Description. Head. Length: 1.20; width across eyes: 1.96; length antennal segments: I, 1.88; II, 1.00; III, 0.80; IV, 1.48; shiny black, with large semi-pedunculate bulging eyes and clothed with silvery pubescence, intermixed with erect hairs; an-



Figs. 1, 2. 1. *Theraneis neotropicalis,* new species. 2. *Theraneis multicoloratus,* new species.

tennal segments I and II shiny black, III and IV reddish black; labium black, reaching anterior margin of metasternum.

Thorax. Pronotum. Anterior lobe: length: 0.88; width: 1.80. *Posterior lobe:* length: 1.16; width: 2.72. Trapezoidal-shaped, shorter than wide, with rounded edges; shiny black, posterior corners creamy yellow and with the following areas covered with adpressed silvery pubescence: anterior margin including collar, anterior half of anterolateral border, wide transverse fascia posteriad to callus, posterior margin (except tip of humeral angle) and a narrow longitudinal median band which bisects posterior lobe; disc with deep and coarse punctation; humeral angles rounded and not exposed; sides and underside of thorax densely clothed with adpressed silvery hairs, except for following shiny black areas: anterior and middle acetabule, an oval or irregular median spot on propleural, mesopleural and metapleural regions, superior margin of propleural, posterior propleural and mesopleural flanks, anterior metapleural flank and two irregular spots laterally to mesosternum; posterior margin of metathorax creamy yellow; legs shiny black, covered with fine adpressed silvery hairs, intermingled with long white setae; tarsal segments reddish brown; metapleural scent-gland orifices with orange black peritreme. *Scutellum.* Length: 1.40; width: 1.32; slightly longer than wide; dull black; anterior part slightly depressed, irregularly punctate and provided with short dense pubescence, intermixed with some erect hairs. *Hemelytra.* Clavus creamy yellow with anal border, claval commissure and claval suture black; corium tricolored, anterior half creamy yellow, except for an elongate triangular black

area close to clavus, followed by a wide orange transverse fascia and a creamy yellow area at posterior end; membrane dark brown.

Abdomen. Connexivum shiny black with some erect hairs; dorsal segments I to VI yellow, with irregular black spots medially; dorsal segments VII to IX shiny black; underside black and densely covered with adpressed silvery pubescence, intermixed with erect hairs; lateral portions of third sternite, posterior margin of seventh sternite and genital plates shiny black. Total body length 9.75.

Holotype. Female. BRAZIL: GOYAZ: Jatahy, 1900, H. Donckier. Deposited in MNP.

Discussion. Recognized by its large size, contrasting coloration of the hemelytra, dorsal abdominal segments I to VI yellowish as well as the pattern distribution of the dorsal and ventral silvery pubescence. This is the only species in the genus for which the color of the posterior margin of metathorax is creamy yellow, the margin of the other species is black.

Etymology. Named for its occurrence in the Neotropical Region.

Theraneis multicoloratus, new species
(Fig. 2)

Male. Description. Head. Length: 0.92; width across eyes: 1.64; length antennal segments: I, 1.52; II, 0.80; III, 0.56; IV, 1.36; black, with large semi-pedunculate bulging eyes and clothed with silvery pubescence, intermixed with erect hairs; antennal segments I to III black, IV dark orange chestnut brown; labium black, reaching mesocoxae.

Thorax. Pronotum. Anterior lobe: length: 0.72; width: 1.48. *Posterior lobe:* length: 1.00; width: 2.16. Trapezoidal-shaped, shorter than wide, with fairly rounded edges; black, except for posterior corners which are reddish-orange; surface densely set with silvery, adpressed hairs, except the following shiny black areas with only few erect hairs: transverse fascia along anterior lobe and most of posterior lobe (posterior margin and median longitudinal stripe with silvery pubescence); disc with deep and coarse punctation; humeral angles rounded and not exposed; sides and underside of thorax densely clothed with adpressed silvery hairs, except posterior propleural and anterior mesopleural flanks, plus two irregular spots laterally to mesosternum which are shiny black with only some long setae; legs shiny black, covered with fine, adpressed silvery hairs, intermingled with long white setae; tarsal segments black and shiny reddish-brown; metapleural scent-gland orifices with black peritreme. *Scutellum.* Length: 1.28; width: 1.00; slightly longer than wide, dull black, with dark orange chestnut brown apex; anterior part slightly depressed, irregularly punctate and provided with short silvery pubescence intermixed with some erect hairs. *Hemelytra.* Clavus pale yellowish orange; corium tricolored, anterior half pale yellowish orange, followed by a black irregular transverse fascia located beyond claval commissure and followed by pale yellow apical margin and apical angle; membrane dark brown with a narrow dirty white border, and basal angle and adjacent area to apical border of corium dirty yellowish ochre.

Abdomen. Connexivum and venter black, densely covered with adpressed silvery pubescence, intermixed with erect hairs; dorsal segments shiny black; seventh sternite shiny black with erect hairs and with only pleural margin densely covered with silvery

pubescence. *Pygophore.* Postero-ventral border with an open, triangular, shallow notch and with lateral borders thickened. Total body length: 8.58.

Female. Head. Length: 1.04; width across eyes: 1.76; length antennal segments: I, 1.76; II, 0.80; III, 0.68; IV, 1.40. *Pronotum. Anterior lobe:* length: 0.72; width: 1.64. *Posterior lobe:* length: 1.08; width: 2.40. *Scutellum.* Length: 1.44; width: 1.16. Total body length: 9.57. Markings and coloration similar to male.

Holotype. Male. BRAZIL: PARA: Rio Iripi Camp. (52°40′W, 3°50′S) Altamira (ca. 100 km S), 17–18. X. 1986, P. Spangler & O. Flint. Deposited in USNM.

Paratype. Female. Same data. Deposited in IBUNAM.

Discussion. This beautiful species is recognized by the attractive coloration of its hemelytra which alternates a pale yellowish orange region, a black transverse fascia and a pale yellow area. The pattern of pubescence is diagnostic where just a few spots show a shiny black coloration with only few scattered hairs. The characteristic spots are: a transverse fascia along the anterior lobe and most of the posterior lobe of the pronotum; the posterior propleural and the anterior mesopleural flanks of the thorax, plus two lateral areas on the mesosternum and most of the seventh abdominal sternite.

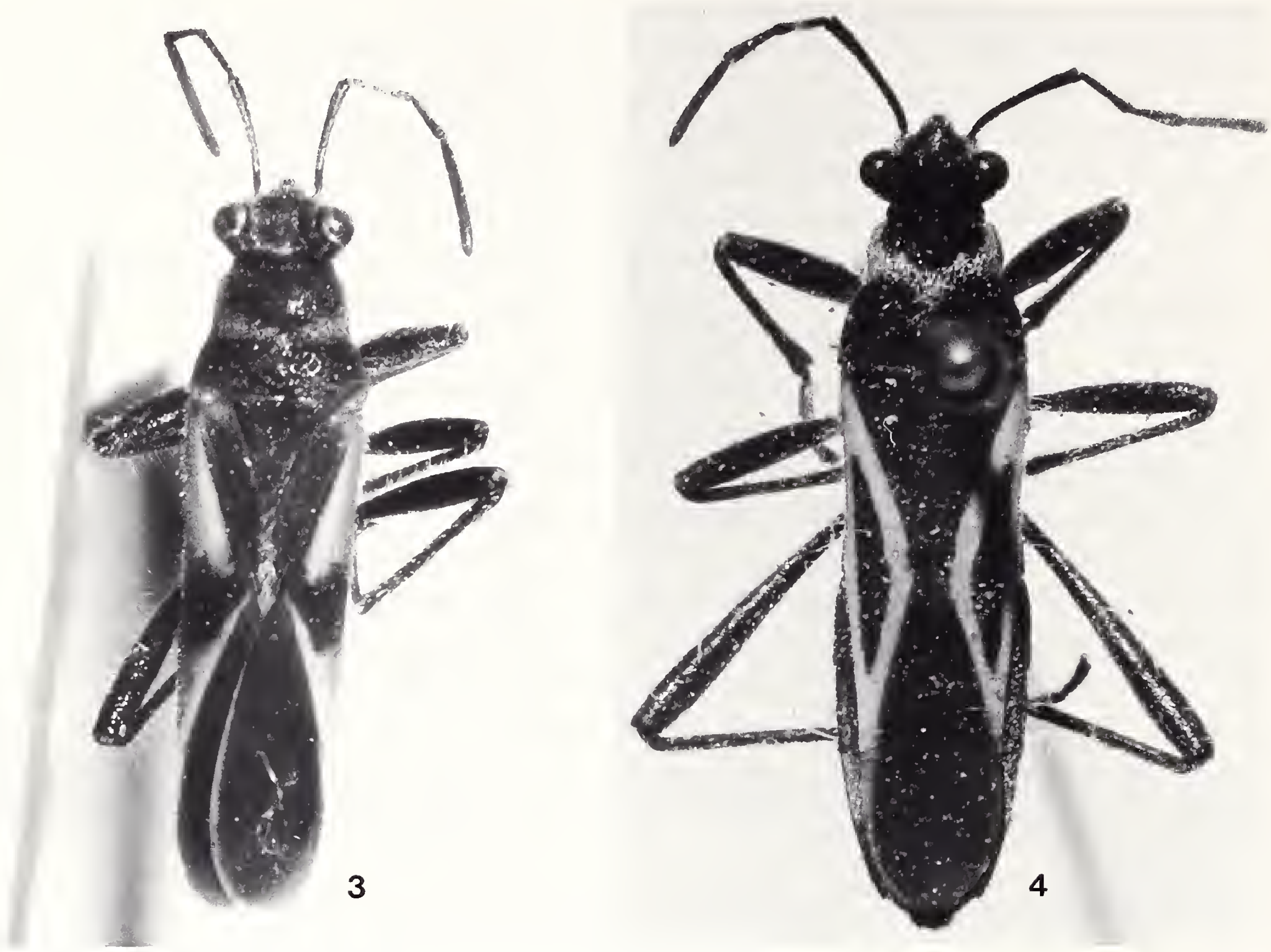
Like *T. surinamensis* Van Doesburg the clavus is unicolorous, the antennal segment II black, the humeral angles inermis and the pronotum black with the humeral angles red, yellow or orange. In *T. multicoloratus,* new species, the corium is tricolored which is the most distinctive feature, whilst in *T. surinamensis* it is completely yellow or orange.

Etymology. Named for the attractive coloration of the corium.

Theraneis araguaensis, new species
(Fig. 3)

Male. Description. Head. Length: 0.96; width across eyes: 1.56; length antennal segments: I, 1.40; II, 0.76; III, 0.56; IV, 1.40; shiny black, with large semi-pedunculate bulging eyes and clothed with scattered silvery pubescence, intermixed with erect hairs; antennal segments I and II shiny black, III shiny reddish-black and IV orange red chestnut-brown; labium black, reaching the mesocoxae.

Thorax. Pronotum. Anterior lobe: length: 0.78; width: 1.48. *Posterior lobe:* length: 0.76; width: 1.92. Trapezoidal-shaped, slightly shorter than wide, with fairly rounded edges; black, posterior corners reddish-orange; posterior sulcus of callus densely set with silvery adpressed hairs; disc with deep and coarse punctation; humeral angles rounded and not exposed; sides and underside of thorax densely clothed with adpressed silvery hairs, except posterior propleural and two irregular spots, laterally to mesosternum which are shiny black with only some long setae; legs shiny black, covered with fine adpressed silvery hairs, intermingled with long white setae; apical tibiae and tarsal segments shiny reddish-black; metapleural scent-gland orifices with black peritreme. *Scutellum.* Length: 1.00; width: 0.92; slightly longer than wide; dull black; anterior part slightly depressed, irregularly punctate and provided with some erect hairs. *Hemelytra.* Clavus black, basal third and anal border reddish-orange; corium tricolored, exocorium including costal margin reddish-orange, endocorium and apical margin creamy yellow and most of the area bordering claval suture and subdiscoidal spot located on middle third near apical margin black or dark brown; membrane dark brown with a complete wide whitish border.



Figs. 3, 4. 3. *Theraneis araguaensis*, new species. 4. *Theraneis elongatus*, new species.

Abdomen. Shiny black with some erect hairs; posterior margins of sternites III to VI densely covered with adpressed silvery pubescence. *Pygophore.* Postero-ventral border U-shaped and thickened. Total body length: 8.28.

Holotype. Male. VENEZUELA: ARAGUA: Rancho Grande, 5.VI. 1958, F. Fernández Yepez. Deposited in UCV.

Discussion. This is the first time the genus *Theraneis* is reported from Venezuela. *T. araguaensis*, new species, is a very distinct species, not only in having the coloration of the hemelytra completely different from that found in the other species, but also the distribution of the silvery adpressed pubescence and the shape of the postero-ventral border of pygophore.

Theraneis pulchra Distant is closely related, resembling *T. araguaensis* in size, shape of humeral angles and general habitus. In *T. pulchra* the clavus and corium are entirely light yellowish-orange or reddish-orange and antennal segment II yellow. In *T. araguaensis* the antennal segments II are black.

Etymology. Named for the type locality, Aragua.

Theraneis elongatus, new species
(Fig. 4)

Male. Description. Head. Length: 1.08; width across eyes: 1.76; length antennal segments: I, 2.00; II, 0.96; III, 0.68; IV, 1.64; black, with large semi-pedunculate bulging eyes and clothed with silvery adpressed pubescence, intermixed with erect

hairs; antennal segments I and II dark reddish-black, III dark orange chestnut-brown and IV little lighter than III; labium black, reaching the mesocoxae.

Thorax. Pronotum. Anterior lobe: length: 0.80; width: 1.60. *Posterior lobe:* length: 0.96; width: 2.16. Trapezoidal-shaped, black, slightly shorter than wide, with fairly straight edges; posterior sulcus of callus densely set with silvery, adpressed hairs; pubescence extending posteriorly into a median longitudinal stripe that reaches the posterior border; disc with deep and coarse punctation; humeral angles not exposed and with a small apical tooth; sides and underside of thorax densely clothed with adpressed silvery hairs, except posterior propleural, posterior mesopleural and anterior metapleural flanks, plus two irregular spots laterally to mesosternum which are shiny black with only some long setae; legs shiny black covered with fine, adpressed silvery hairs, intermingled with long white setae; tarsal segments dark orange reddish-brown; metapleural scent-gland orifices with black peritreme. *Scutellum.* Length: 0.88; width: 0.80; slightly longer than wide, dull black, apex dark reddish-brown; anterior part slightly depressed, irregularly punctate and provided with some erect hairs. *Hemelytra.* Clavus dull black; corium creamy yellow with a longitudinal median black stripe; membrane pale brown, with a wide external whitish border.

Abdomen. Connexivum and venter black and densely covered with adpressed silvery pubescence, intermixed with erect hairs; dorsal segments shiny black; pleural margin of sternal segments III to V and VII, posterior margin of sixth sternite and seventh sternite shiny black, with erect hairs and with only the posterior margin of seventh sternite densely covered with silvery pubescence. *Pygophore.* Postero-ventral border rounded and entire. Total body length: 8.73.

Female. Head. Length: 1.20; width across eyes: 1.84; length antennal segments: I, 2.12; II, 1.00; III, 0.76; IV, 1.60. *Pronotum. Anterior lobe:* length: 0.76; width: 1.68. *Posterior lobe:* length: 1.20; width: 2.36. *Scutellum.* Length: 0.96; width: 0.88. Total body length: 10.22. Markings and coloration similar to male.

Holotype. Male. PERU: Satipo, 10. VIII. 1941. P. Paprzcki. Deposited in USNM.

Paratype. One female with the same data. Deposited in USNM. One female PERU: TINGO MARIA: Rio Huallaga, VII. 1947, W. Weyrauch. Deposited in IBUNAM.

Discussion. This unique species can be distinguished by having a light creamy yellow corium with a longitudinal black band that runs almost throughout the corial disk and the ventral distribution of the silvery pubescence.

In *T. lurida* Distant, a closely related species, the humeral angle also has a small tooth, but in *lurida* the clavus and corium are entirely light orange-yellow.

Etymology. Named for its elongate black stripe of the corium.

TENTATIVE KEY FOR MOST OF THE KNOWN SPECIES OF *THERANEIS* SPINOLA*

1. Hemelytral membrane not reaching apex of abdomen .... *T. amabilis* Breddin
1′. Hemelytral membrane reaching or beyond apex of abdomen 2
2. Humeral angles of the pronotum provided with large and acute spine directed towards the back .... *T. spinosa* Distant
2′. Humeral angles of the pronotum without large and acute spine 3
3. Humeral angles of the pronotum with a small, obtuse apical tooth, directed towards the back 4

* *T. constricta* Stål, *T. isobel* Hussey and *T. ferruginea* Mayr are excluded.

3′. Humeral angles of the pronotum inermis 5
4. Clavus and corium orange or yellow .... *T. lurida* Distant
4′. Clavus black; corium creamy yellow with longitudinal median black stripe .... *T. elongatus,* new species
5. Antennal segment II yellow 6
5′. Antennal segment II black 7
6. Clavus black .... *T. montivaga* Schmidt
6′. Clavus yellow or orange .... *T. pulchra* Distant
7. Pronotum black, densely silver pubescent, with the humeral angles red, or yellow, or orange or creamy yellow 8
7′. Anterior lobe of the pronotum black and posterior lobe yellow or orange or with a mixture of black and yellow or orange 13
8. Posterior margin of metathorax creamy yellow .... *T. neotropicalis,* new species
8′. Posterior margin of metathorax black 9
9. Clavus unicolorous, entirely pale orange or yellow 10
9′. Clavus bicolorous 11
10. Corium unicolorous, entirely yellow or orange .... *T. surinamensis* Van Doesburg
10′. Corium tricolored, with anterior half pale orange yellowish, followed by black and irregular transverse fascia located below claval commissure and rest which includes pale yellow apical margin and apical angle .... *T. multicoloratus,* new species
11. Corium yellow or orange and only with the internal angle below the claval suture black .... *T. vaga* Schmidt
11′. Corium with another condition 12
12. Corium with three longitudinal bands, the external light orange, middle one yellow and the internal black .... *T. vittata* Spinola
12′. Corium with two longitudinal bands, the external light orange and internal creamy yellow, broken in the middle by a transversal, irregular black band .... *T. araguaensis,* new species
13. Posterior lobe of the pronotum yellow or orange .... *T. oleosa* Distant
13′. Posterior lobe of the pronotum yellow, with large black spots on either side .... *T. dissimilis* Distant

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A GENETIC MARKER FOR INVESTIGATING PATERNITY AND MATERNITY IN THE BURYING BEETLE *NICROPHORUS ORBICOLLIS* (COLEOPTERA: SILPHIDAE)

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Abstract.—A purebred "spotless" line of *Nicrophorus orbicollis* was produced by inbreeding. Spotless beetles completely lack orange markings on the basal portion of the elytra. The spotless trait appears to be largely under the influence of a single gene and is an excellent genetic marker for paternity or maternity in a variety of competitive breeding situations. In the laboratory, individuals possessing the spotless trait were as reproductively successful as normally marked beetles. The spotless marker was used to demonstrate that males which pair with a female achieve a high level of paternity. Paternity remained high in a second brood even when the male was separated from the female in the interval between reproductive attempts.

The ability to assign paternity and maternity has become nearly essential in behavioral studies of reproductive success. Three prominent techniques include: sterilization of males, molecular genetic comparisons (e.g., electrophoresis and DNA fingerprinting) and phenotypic markers. In many situations, phenotypic markers are ideal because subjects do not have to be handled or sacrificed and the employment of the technique has limited effect on behavior or vigor.

One important application of genetic markers has been to the study of sperm competition, a process in which ejaculates of more than male compete for fertilization of an egg (Parker, 1970). In the majority of insects investigated the last male to mate fathers a high proportion of the brood (Parker, 1970; Gwynne, 1984). A strong correlation between paternity and male parental care has been noted (Ridley, 1978; Alexander and Borgia, 1979) despite the fact that there are no theoretical reasons why a high level of paternity itself should promote paternal care (Maynard Smith, 1978; Werren et al., 1980). Once paternal care has evolved, however, paternity-enhancing mechanisms which require extended male-female contact can be selected (Werren et al., 1980; Knowlten and Greenwell, 1984).

The need to employ genetic markers to investigate sperm competition and other aspects of reproductive competition in *Nicrophorus* is evident because of the complexity of social interactions. Males and females arrive at small vertebrate carcasses and compete intrasexually for the right to breed. The dominant male and female bury the carcass, remove any hair or feathers and roll the carcass into a ball (Pukowski, 1933). Courtship is minimal and mate choice appears to be entirely passive (Milne and Milne, 1976; Otronen, 1988). If a male fails to discover the carcass a female will breed on her own using stored sperm (Bartlett, 1988; Scott, 1989; Trumbo, 1990a). Females have acquired sperm by copulating with males that emit pheromones in the absence of a carcass or by copulating with males on large carcasses where only feeding occurs (Müller and Eggert, 1987; Eggert and Müller, 1990). When more than one

male discovers the carcass, the subordinate male can adopt a satellite strategy and obtain some reproductive success despite being forced off the carcass by the dominant male (Bartlett, 1988). Subordinate females that are displaced from the carcass also can achieve some reproductive success by brood parasitism (Müller et al., 1990). The resident male fathers 92% of offspring in *N. vespilloides* by copulating repeatedly with the female prior to and throughout oviposition (Müller and Eggert, 1989). Once larvae appear on the carcass, they are fed and guarded by both parents (Bartlett, 1988; Scott, 1990; Scott and Traniello, 1990). The male usually deserts before the female and both sexes can attempt reproduction a second or third time in the breeding season.

In this paper we describe a phenotypic marker ('spotless') for *N. orbicollis* Say that can be used to determine either paternity or maternity, examine the genetic basis of the marker, compare the reproductive success of two stocks possessing alternative genetic markers and apply the marker in an initial sperm competition experiment.

METHODS

Genetic basis of the marker. A single *Nicrophorus orbicollis* male completely lacking orange basal markings of the elytra was caught on a mouse carcass at The University of Michigan Biological Station in 1986 and subsequently bred to three normally marked females. All beetles were reared and bred at 19–22°C and a 15L:9D cycle. These hybrid offspring were crossed and the resulting F_2 population contained approximately one-quarter spotless individuals. Additional normal × normal crosses were made to produce an F_2 laboratory population of normally marked beetles. Nine different types of crosses were then made using these F_2 stocks and hybrid F_3 individuals (hybrid individuals always had some degree of marking on the basal portion of the elytra). Females were isolated a few days after adult emergence and paired with males 1 day prior to trials. These pairs were placed in 8 × 15 × 30 cm containers filled with soil and provided a mouse carcass (21–30 g). Progeny from a total of 87 crosses were reared to the adult stage and scored as spotted (having some degree of basal marking) or spotless.

Comparative reproductive success. The spotless stock was maintained through inbreeding and outcrossed in 1987 to field caught beetles. The resulting hybrid progeny were crossed to start a new spotless laboratory population. The outcrossing procedure was an attempt to avoid inbreeding depression in our laboratory populations. Additional normal × normal crosses were made using field caught beetles to start a new laboratory population of normally marked beetles. To compare the reproductive performance of these two new stocks, 17 normal × normal crosses and 18 spotless × spotless crosses were made using 25–30 g mouse carcasses as a breeding resource for each pair. Larvae were counted and the mass of the brood was determined at the time larvae dispersed from the nest.

Paternity of the resident male. The spotless stock was again outcrossed and a new spotless laboratory population was started from progeny of hybrid × hybrid crosses. The laboratory population of normally marked beetles was maintained and kept in reproductive synchrony with the spotless population. A few days after adult emergence groups of 5 spotless females were placed into containers with either 5 normal males or 5 spotless males. At 22–28 days females were paired with a male of the

Table 1. Frequency of phenotypes resulting from test crosses.

Presumed genotype of male parent[1]	Presumed genotype of female parent	Number of crosses	Phenotype of offspring				G[2]
			Spotless male	Spotless female	Normal male	Normal female	
spl-spl	*spl-spl*	18	106	122	0	0	—
nor-nor	*nor-nor*	6	0	0	30	33	—
spl-nor	*spl-nor*	20	28	29	81	92	0.01*
spl-spl	*nor-nor*	6	0	0	32	22	—
nor-nor	*spl-spl*	5	0	0	24	28	—
spl-spl	*spl-nor*	14	34	43	26	34	2.11**
spl-nor	*spl-spl*	10	30	28	28	37	0.40*
nor-nor	*spl-nor*	3	0	0	16	19	—
spl-nor	*nor-nor*	4	0	0	21	27	—

[1] *spl-spl* were spotless beetles; *nor-nor* were normally marked beetles; and, *spl-nor* were offspring of known *spl-spl* × *nor-nor* crosses.

[2] G values computed by comparing the observed frequency of phenotypes with the expected frequency based on a one gene model for the trait: * $P > 0.2$; ** $P > 0.1$.

alternative genetic marker and each pair was provided a mouse carcass (21–24 g) on which to breed. Larvae were counted and weighed as before and paternity was determined after adult emergence. Parents were separated after larvae dispersed and 5 days later each isolated female was provided a second 21–24 g carcass. Resulting progeny were counted and weighed at larval dispersal and paternity was determined by examining offspring at the adult stage.

RESULTS

All types of crosses involving normal, spotless and hybrid beetles produced offspring whose phenotype could be scored as either spotted or spotless. The distribution of phenotypes among offspring suggests that a single gene is primarily responsible for the spotless mutation such that a homozygote individual completely lacks orange markings on the basal portion of the elytra (Table 1). Heterozygote individuals, however, varied considerably in the degree of basal marking and could not be distinguished reliably from homozygote normal beetles.

In the second experiment, 16 of 17 normal × normal crosses and 16 of 18 spotless × spotless crosses produced offspring. Neither the mean (±SE) number of larvae at dispersal (12.88 ± 1.28 vs. 12.56 ± 1.29, F = 0.11, ns) nor the mean (±SE) mass of broods (5.49 ± 0.51 g vs. 5.28 ± 0.35 g, F = 0.29, ns) differed between normal × normal and spotless × spotless crosses, respectively.

A male that pairs with a female on the carcass and copulates throughout the oviposition period achieves a high degree of paternity (93% of total offspring in first broods, Table 2). The genotype of a paired male, and the genotype-reproductive attempt interaction were not related significantly to either the number of larvae or the mass of the brood. Second reproductive attempts had significantly more larvae and a larger brood mass than first reproductive attempts. Paternity of paired males remained high (96% of total offspring in second broods) even though females were

Table 2. Success in first and second reproductive attempts for *spl-spl* females initially paired with normally marked (*nor-nor*) or spotless (*spl-spl*) males.

	nor-nor male		*spl-spl* male	
	First attempt	Second attempt	First attempt	Second attempt
Mean (±SE) number of offspring	9.67 (1.36)	13.63 (0.71)	10.00 (1.05)	12.67 (0.62)
Mean (±SE) mass of brood	4.20 (0.67)	5.79 (0.27)	4.74 (0.40)	5.29 (0.20)
Proportion of mixed broods	0.33	0.25	0.22	0.33
Mean proportion of brood attributed to the paired male	0.92	0.98	0.91	0.95

Two-way ANOVAs performed to test effects of Male Genotype (MG) and Reproductive Attempt (RA). Number of offspring: $F_{MG} = 0.10$, ns; $F_{RA} = 11.00$, $P = 0.002$; $F_{MG \times RA} = 0.42$, ns. Mass of brood: $F_{MG} = 0.00$, ns; $F_{RA} = 6.03$, $P = 0.02$; $F_{MG \times RA} = 1.43$, ns. Proportion (arcsin transformed) of brood attributed to paired male: $F_{MG} = 0.05$, ns; $F_{RA} = 0.30$, ns; $F_{MG \times RA} = 0.15$, ns.

isolated from males between reproductive attempts and subsequently reproduced on their own.

DISCUSSION

The spotless trait is an unambiguous genetic marker that permits the identification of paternity or maternity in competitive breeding situations involving appropriate individuals. The trait is largely controlled by a single gene although variation among heterozygote and homozygote normal beetles suggests that additional genes or the environment are involved in determining the extent of marking on the basal portion of the elytra. The use of this genetic marker has been employed to demonstrate that both male and female burying beetles obtain reproductive benefits following infanticide (Trumbo, 1990b). Similar elytral pattern markers have been used to demonstrate intraspecific brood parasitism in *N. vespilloides* (Müller et al., 1990). Anderson and Peck (1986) examined variation in elytral patterns across North American species of *Nicrophorus* and found that melanic forms were most common on the Pacific Northwest coast. They speculate that melanism might play a role in thermoregulation in localities with lower levels of solar radiation. Presumably the tradeoff of melanism is less protection from predators since the bright orange marks on the elytra are thought to function as aposematic warning coloration. If true, elytral pattern variation is an excellent marker for comparing reproductive success in laboratory situations not involving predation.

Males of *N. vespilloides* and *N. orbicollis* that pair with a female obtain a high level of paternity (Bartlett, 1988; Müller and Eggert, 1989) as is common among insects with paternal care (Alexander and Borgia, 1979). As in male brooding water bugs, the paternity-enhancing mechanism is repeated copulation before and throughout oviposition (Smith, 1979; Müller and Eggert, 1989). This strategy is especially effective when females mate with other males between copulatory attempts by the dominant male (Thornhill and Alcock, 1983), a situation that likely occurs in *Nicrophorus* (Wilson and Fudge, 1984; Bartlett, 1988).

When competitors are not present, a *Nicrophorus* female that attempts to breed

on her own achieves equal or greater reproductive success than pairs (Bartlett, 1988; Scott, 1989; Trumbo, 1990a). To reproduce successfully without the help of a male, a female must periodically obtain fresh sperm from a male because sperm become inviable; in *N. vespilloides,* 16% of sperm were inviable after 14 days and 43% were inviable after 21 days (Eggert and Müller, 1989). It is unclear whether the high level of paternity that males obtained in the second reproductive attempt was due to a lack of sperm mixing or the inviability of sperm from previously mated males (sperm from previous males were approximately 16 days old at the start of the second reproductive attempt). The more common pattern in insects is for mixing to occur with time (Schlager, 1960; Siva-Jothy and Tsubaki, 1989). A high degree of paternity is obtained in some species by flushing or removal of previously deposited sperm (Waage, 1979; Parker, 1984) but this does not appear compatible with the male burying beetle strategy of mating as many as 100 times during the oviposition period (Müller and Eggert, 1989). By whatever mechanism, a male that stays with a female throughout oviposition might obtain an additional reproductive benefit if the female completes the present reproductive attempt and subsequently breeds on her own.

Second reproductive attempts produced more larvae and a larger brood than first reproductive attempts, contrary to results reported previously (Scott and Traniello, 1990; Trumbo, 1990c). Scott (1989) found that the presence of a male decreased reproductive success if the male was confined to the nest area until larvae dispersed, but a male does not have a negative effect if he is removed or allowed to escape by day 9 (Scott, pers. comm.; Trumbo, 1991). Since the male was retained in breeding containers in our study, this might provide one explanation for lower reproductive success in first reproductive attempts.

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A NEW SPECIES OF *OPHRAELLA* WILCOX (COLEOPTERA: CHRYSOMELIDAE) FROM THE SOUTHEASTERN UNITED STATES

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Abstract.—*Ophraella slobodkini,* new species, is described from the southeastern United States. It shares the host association of *Ambrosia artemisiifolia* with *O. communa* LeSage, but is a sibling species of *O. notulata* Fabricius. The three species can be statistically distinguished using morphological characters, and reliably distinguished by electrophoretic mobility of several enzymes.

Ophraella (Wilcox, 1965) is a North American genus of leaf beetles (Chrysomelidae: Galerucinae, Galerucini), the species of which are specifically associated with various Asteraceae (Compositae). Among the currently recognized species (LeSage, 1986, Futuyma, 1990), one is associated with *Iva frutescens* (marsh elder) along the Atlantic and Gulf coasts, and another is associated with *Ambrosia artemisiifolia* (common ragweed) throughout much of North America. LeSage (1986) applied the name *notulata* Fabricius to the *Iva*-associated species, which had hitherto been referred to *integra* LeConte, and designated as *Ophraella communa* LeSage the *Ambrosia*-associated species, which prior to LeSage's work had borne the epithet *notulata.* In the course of a study of the evolution of host associations in *Ophraella* (Futuyma, 1990; Futuyma and McCafferty, 1990), an undescribed species has come to light. Although it shares the host association (*Ambrosia artemisiifolia*) of *O. communa,* it is a sibling species of *O. notulata,* from which it is statistically distinguishable by a few morphological features, and reliably distinguishable by the electrophoretic mobility of several enzymes. In appreciation of my mentor and colleague, the ecologist Lawrence B. Slobodkin, I gratefully designate it

Ophraella slobodkini, new species

Diagnosis. Morphologically, this species is indistinguishable from *Ophraella notulata* (Fabricius) except by the following differences which characterize many but not all specimens. The anterior margin of the labrum is slightly concave; in a minority of specimens it is even or slightly convex, the usual condition in *O. notulata.* The pronotum is anteriorly usually glabrous (extending to ca. 10% of the distance from the margin), whereas it is usually fully setiferous in *O. notulata.* In some but not all populations of *O. slobodkini,* crossbars of dark pigment often extend between the subsutural and cubital ("supplementary" of LeSage, 1986) elytral vittae (rarely so in *O. notulata*). Slight differences in shape between these species will be noted below. The only known host of *O. slobodkini* is *Ambrosia artemisiifolia,* whereas *O. notulata* is only known to feed on *Iva frutescens* and *I. annua.*

Description of imago. Size: Linear measurements (mean and standard deviation, in mm, measured with ocular micrometer; N = 35 pinned females and 36 males from several locations as listed below): Total length (front of head to apex of elytra, in dorsal view) of females 4.96 ± 0.222, of males 4.35 ± 0.231; length of elytra (base of humerus to apex) of females 3.95 ± 0.179, of males 3.45 ± 0.152; width of pronotum of females 1.59 ± 0.058, of males 1.43 ± 0.057; maximal width of left elytron of females 1.35 ± 0.068, of males 1.13 ± 0.061.

Coloration: Ground color yellowish brown (testaceous). Dark brown to black coronal mark, apices of antennomeres and leg segments, labrum (except base), and venter (variably testaceous to piceous). Pronotum with a dark medial macula, a lateral macula, and in some specimens a small macula lateral to the latter. Each elytron with four dark brown to black vittae: lateral vitta extending from base of humerus nearly to apex, joining the subsutural vitta; subsutural vitta extending fully to base or becoming evanescent in basal quarter; discal vitta extending from base to apex, usually approaching or joining the subsutural; cubital (supplementary) vitta extending obliquely toward suture from base to apex, confluent with subsutural vitta at about 70% of the distance from the base and forming a single vitta thereafter; cubital and subsutural vittae frequently joined by dark crossbands at base and more distally, these expanded in some specimens, leaving only small windows between the almost fully confluent vittae. Some specimens with interruptions in discal, cubital, and/or subsutural vittae, and with the discal vitta weak or evanescent basally and apically.

Setation and punctation: Setae of head dense on vertex, sparser on frons and genae; frontal tubercules glabrous, slightly punctate; pronotum dorsally with fairly dense setae except near anterior margin, coarsely punctate, the punctures confluent posteriorly; elytra densely and evenly invested with short, fine, recumbent setae and bearing sparse erect setae, especially posteriorly along vittae; setae of epipleuron sparser; elytral punctures dense, very small, separated by distances equal to or slightly greater than their diameter, slightly larger basally, their pattern not altered in vicinity of vittae.

Other structural features: Pronotum rather flat, explanate rather than arched, broadest at or slightly behind middle, lateral margins evenly convex or almost straight before the middle, anterior margin slightly concave, posterior margin sinuous, medially concave. Posterior margin of scutellum convex. Setae of mouthparts (each side): prementum 1; cardo 1–3 (mode = 1), apicolateral; maxillary palpifer 1 or 2 (mode = 1); labrum with 5 small lateral setae on anterior margin. Mandible lacking visible setae or serrations on margin of teeth. Sternum VIII of female (LeSage, 1986) shallowly emarginate at apex, with a broad stem between the lateral wings and the laterally extended base; mean ratio of stem width to sternum length 0.79 (N = 4), ratio of breadth across wings to length 1.15. Spermatheca narrow throughout, with receptacle and pump hardly inflated; apex of spermathecal pump simple, lacking appendage. Sternum VIII and spermatheca closely resembling condition in *O. notulata* (LeSage, 1986, figs. 72, 78). Male genitalia indistinguishable from *O. notulata* (LeSage, 1986, fig. 69); sexual dimorphism in visible terminal tergum and sternum, and other characters generally, as in other members of the genus (LeSage, 1986).

Type material. Holotype, female: Florida, Leon Co., 30°39′30″N, 84°12′30″W, 6.5 km west of Iamonia, at Tall Timbers Research Station, elevation 45 m, Douglas J. Futuyma, collector, 24 April 1989. Paratypes: Nineteen specimens with data as for

the holotype. Holotype (C. U. type number 6505) and paratypes deposited in the Cornell University Insect Collection, Ithaca, New York.

Other deposited material. (Unless otherwise noted, all were collected by the author, with assistance from M. Keese.) Georgia, Thomas Co., Thomasville, 24 April 1989 (2 specimens); Florida, Escambia Co., Co. Rd. 293, ca. 19 km W of Pensacola, 22 May 1986 (1); Florida, Duval Co., Lawtey, 20 April 1989 (5); Florida, Flagler Co., Bunnell, 21 April 1989 (15); Florida, Broward Co., Merritt Island National Wildlife Refuge, 21 April 1989 (20); Florida, Pasco Co., Slaughter (in Withlacoochee National Forest), 22 April 1989 (20); Florida, Broward Co., Dania, 24 December 1988 (35), 13 December 1985 (3, coll. D. Furth). All specimens, including type series, collected on *Ambrosia artemisiifolia.* Deposited as follows: Cornell University Insect Collection (Thomasville, Ga., 2; Bunnell, Fla., 10; Slaughter, Fla., 5; Merritt Island NWR, Fla., 10; Lawtey, Fla., 5; Escambia Co., Fla., 1; Dania, Fla., 10), American Museum of Natural History, New York (Merritt Island NWR, 5; Dania, 5), U.S. National Museum, Washington (Slaughter, 5; Dania, 5), Florida State Collection of Arthropods, Gainesville (Merritt Island NWR, 5; Slaughter, 5; Dania, 5), Museum of Comparative Zoology, Harvard University (Bunnell, 5; Dania, 5), Canadian National Collection, Ottawa (Slaughter, 5; Dania, 5). Some specimens are retained by the author at the State University of New York at Stony Brook.

Morphological and electrophoretic distinctions among Ophraella slobodkini, O. notulata, *and* O. communa. The larvae of *O. slobodkini* appear indistinguishable from those of *O. notulata* and *O. communa* in all characters examined, including mouthparts and setation. Larvae of *O. notulata* in the north (New York, New Jersey) have broad, almost coalescent vittae, but in specimens from Florida, the vittae are narrower and do not distinguish this species from *O. slobodkini.* The adults of *O. slobodkini* and *O. notulata* are statistically distinguishable only by the characters noted in the diagnosis and by shape, as noted below. *Ophraella communa,* which also feeds on *Ambrosia artemisiifolia,* is distinguishable from *O. slobodkini* by its pattern of elytral vittae (the cubital vitta is directed more abruptly toward the subsutural vitta, and terminates in or near it about halfway from the base), by its broader shape (see below), by its longer, more erect, and more variously oriented elytral setae, by its larger elytral punctures, by the greater number of setae on the cardo ($\bar{x}$ = 5.5) and maxillary palpifer ($\bar{x}$ = 2), and by the form of the spermatheca and sternum VIII in the female (LeSage, 1986, figs. 101, 107).

Compared to *Ophraella notulata,* in *O. slobodkini* the pronotum and elytra are slightly, although statistically significantly, broader relative to elytron length (Table 1), the hind tibia is relatively longer, and the pronotum is broader relative to the width across the humeri. *Ophraella slobodkini* has relatively narrower elytra than *O. communa,* which lies between *O. slobodkini* and *O. notulata* in the relation of pronotum breadth to elytron length and breadth across the humeri. The slope of most of these relationships, which are nearly isometric within species, does not differ significantly.

To correct for correlations among these several measurements, multivariate analyses were performed (by D. Slice), using all variables in Table 1 except tibia length (because of missing data). Data were entered separately for the sexes (sample sizes for females and males, respectively, were 34, 36 *O. slobodkini,* 18, 21 *O. notulata,* 17, 22 *O. communa*). Each measurement was $\log_e$-transformed to achieve normal distributions, and was divided by the arithmetic mean of the individual's several

Table 1. Regression equations for pairs of linear measurements (in micrometer units, at 18×) on *Ophraella slobodkini, O. notulata,* and *O. communa.* Tests for significant differences between species in slope and in mean values of Y adjusted to common X are based on analyses of covariance (Sokal and Rohlf, 1981). Sample of *O. slobodkini* is of specimens from Iamonia, Bunnell, Slaughter, Merritt Island NWR, and Dania, Florida; of *O. notulata,* from Citrus and Dixie Co., Fla. (7), Bluffton, S.C. (23), and Tuckerton, N.J. (9), of *O. communa,* from Iamonia, Fla. (10), Thomasville, Ga. (11), and Suffolk Co., N.Y. (18). Sex ratios are approximately 1:1 for all species.

Species	N	$MS_{Y \cdot X}$	Regression equation	Comparison[1]	Difference between adjusted means F	Difference between adjusted means *P*	Difference between adjusted slopes F	Difference between adjusted slopes *P*
1. Maximum breadth of elytron (Y) vs. length of elytron (X)								
O. slobodkini	70	0.990	$Y = -6.207 + 0.419X$	s/n	15.343	0.001	0.151	n.s.
O. notulata	39	1.242	$Y = -8.114 + 0.432X$					
O. communa	39	0.762	$Y = 1.420 + 0.329X$	s/c	24.152	0.001	9.020	0.005
2. Breadth of pronotum (Y) vs. length of elytron (X)								
O. slobodkini	70	0.596	$Y = 7.823 + 0.304X$	s/n	34.537	0.001	1.181	n.s.
O. notulata	39	1.117	$Y = 4.284 + 0.336X$					
O. communa	39	1.346	$Y = 5.495 + 0.343X$	s/c	7.953	0.010	1.800	n.s.
3. Breadth of elytron (humerus to suture) (Y) vs. breadth of pronotum (X)								
O. slobodkini	70	0.438	$Y = -0.286 + 0.685X$	s/n	7.221	0.025	0.945	n.s.
O. notulata	39	0.663	$Y = 2.100 + 0.621X$					
O. communa	39	0.403	$Y = 0.849 + 0.675X$	s/c	37.271	0.001	0.037	n.s.
4. Length of hind tibia (Y) vs. length of elytron (X)								
O. slobodkini	66	1.729	$Y = 15.357 + 0.280X$	s/n	26.571	0.001	4.962	0.050
O. notulata	39	1.479	$Y = 6.146 + 0.379X$					

[1] Comparisons are among *O. slobodkini* (s) and *O. notulata* (n) or *O. communa* (c).

log-transformed measurements. The latter procedure corrects for differences in size, so that the standardized measurements describe shape. A multivariate analysis of variance (not shown) on the standardized measurements indicated statistically significant differences in shape between sexes and among species (the sex by species interaction was not significant). The shape differences among species and sexes are displayed in Figure 2, which presents the first two canonical variates from a canonical discrimination analysis (using the CANDISC procedure of SAS), in which the within-group variances were standardized to 1.0. The sexes (open vs. closed symbols) are largely discriminated by canonical variate 2, whereas both variates, especially variate 1, discriminate the species. The shape of *O. slobodkini* is intermediate between that of *O. notulata* and *O. communa,* although closer to and overlapping *O. notulata.*

Sibling species are frequently most definitively distinguished by enzyme electrophoresis (Menken, 1989). Several enzymes offer the most diagnostic differences between *Ophraella slobodkini* and *O. notulata,* and provide clear evidence that they are distinct species (Table 2). These species are almost fixed for different alleles at the faster of two isocitrate dehydrogenase loci (IDH2), and the most common allele of glucose phosphate isomerase (GPI) in *O. slobodkini* is absent in *O. notulata.* In addition, allele frequencies differ strongly at the leucine aminopeptidase (LAP) locus. These differences hold for syntopic samples of the two species taken from their respective host plants at Merritt Island National Wildlife Refuge and in Dixie Co., Florida, and for samples taken 75 km apart in northern Florida (*O. slobodkini* at Tall Timbers Research Station in Leon Co., *O. notulata* near Panacea in Wakulla Co.). No specimens were electrophoretically misclassified with respect to host plant of origin. Multilocus electrophoretic profiles revealed no evidence of hybridization.

Ophraella slobodkini is distinguished from *O. communa* not only by morphological but also by electrophoretic characters. Allele frequencies differ strongly at the GPI. IDH1 (slower of two loci), IDH2, anodal malate dehydrogenase (MDH1), cathodal aspartate aminotransferase (AAT2), and LAP loci (Table 2). In Table 2, allele frequencies in a sample of *O. slobodkini* from Tall Timbers Research Station near Iamonia, Fla., are compared with *O. communa* taken from the same fields, and from two localities in Georgia, 29 km and 105 km, respectively, northeast of Iamonia. In these samples, completely diagnostic differences are evident at loci IDH1, IDH2, and MDH1. No evidence of hybridization was observed.

Discussion. At all the enzyme loci described above, electromorphs conform to Hardy-Weinberg genotype frequencies within populations both of these and other species of *Ophraella* (Futuyma, 1990; Futuyma and McCafferty, 1990), providing evidence that they are genetic variants. The complete absence of heterozygotes for diagnostic alleles at certain of these loci, even in syntopic or nearly syntopic samples taken from *Ambrosia* and *Iva,* indicates that *O. slobodkini* and *O. notulata* are reproductively isolated sibling species, between which there is little or no gene exchange. Studies in progress by M. C. Keese at Stony Brook indicate that in the laboratory, mating is strongly assortative, and that both adults and hatchling larvae strongly prefer their own host plant in choice tests. These are sister species, sharing synapomorphic states of several morphological characters (the broad eighth sternum of the female, narrow spermathecal receptacle, reduced number of setae on the cardo, extension of the cubital vitta nearly to the apex of the elytron) and electrophoretic characters (Futuyma and McCafferty, 1990). A cladistic analysis of *Ophraella,* based

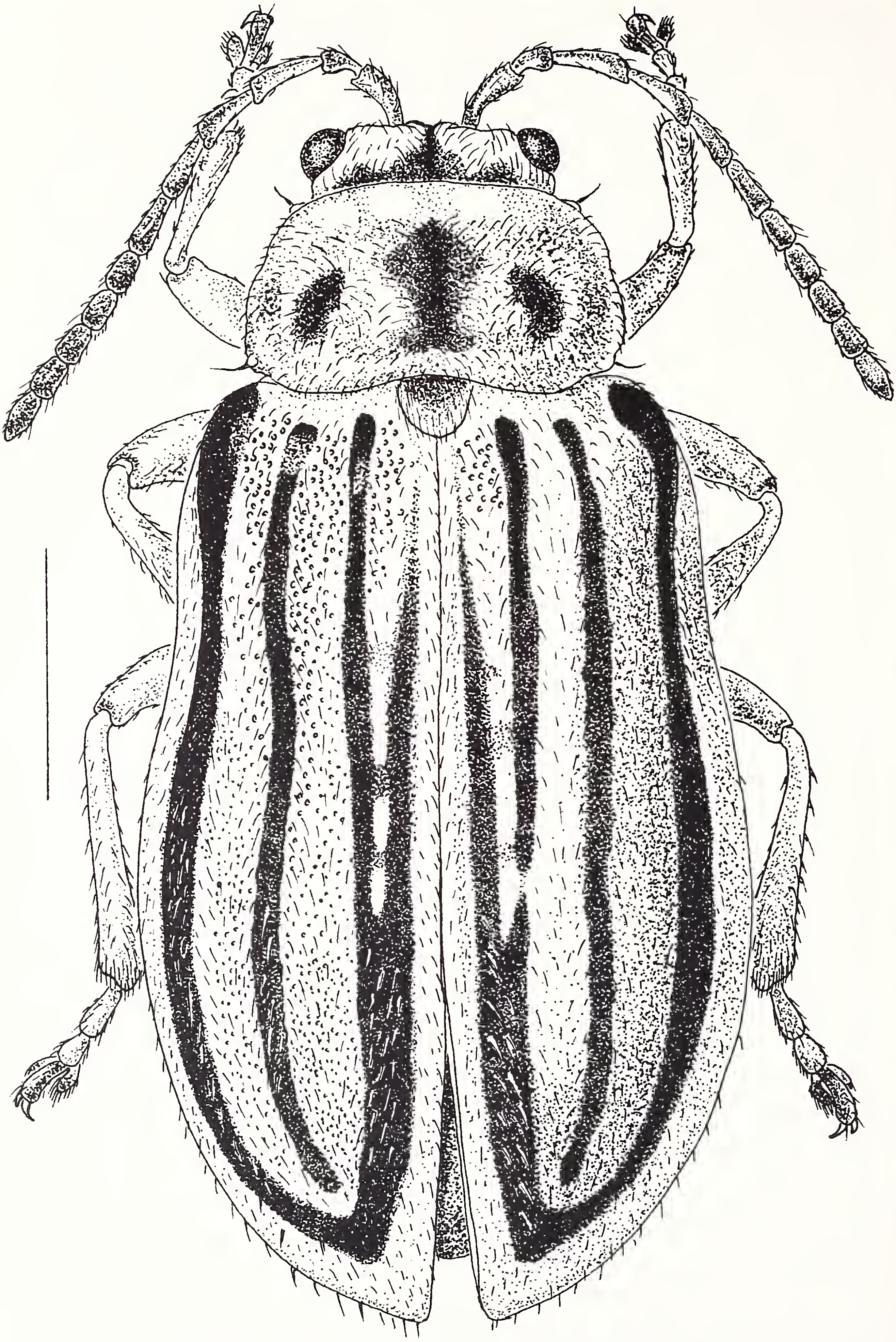

Fig. 1. *Ophraella slobodkini,* female, Slaughter, Withlacoochee National Forest, Pasco Co., Florida, 22 April 1989. Bar = 1 mm.

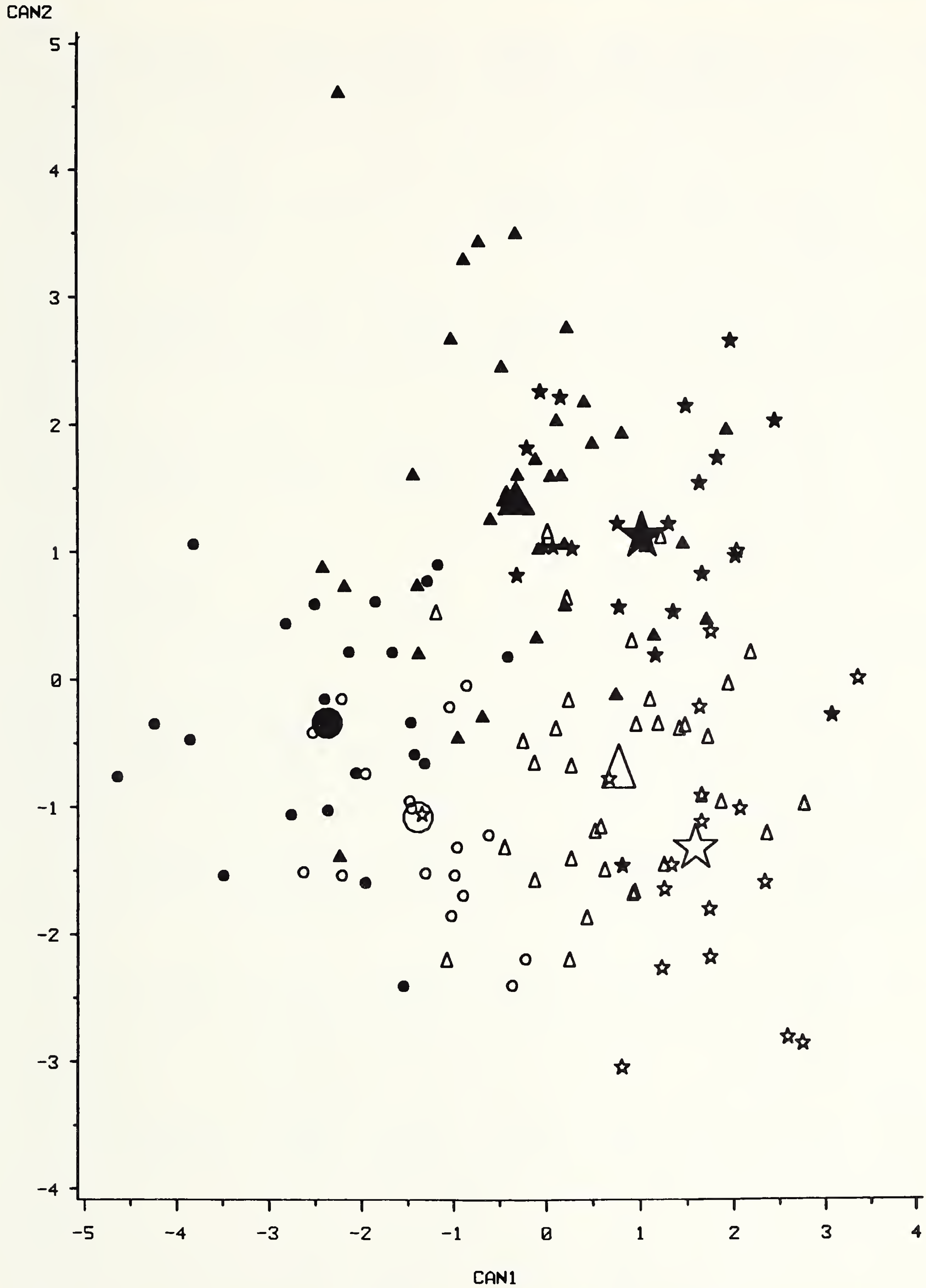

Fig. 2. Canonical discrimination of *Ophraella slobodkini* (triangles), *O. notulata* (stars), and *O. communa* (circles). Open and solid symbols represent individual females and males respectively, and larger symbols represent joint means of the first two canonical variates, which describe two dimensions of shape differences, to each of which several measurements contribute. Axes are marked in unit standard deviations.

Table 2. Allele frequencies at loci showing pronounced frequency differences among *Ophraella slobodkini*, *O. notulata*, and *O. communa*. The first two columns give pooled frequencies for samples of *O. slobodkini* from throughout Florida and for samples of *O. notulata* from localities in Florida and Louisiana. The other columns give frequencies for sympatric or nearly sympatric populations of *O. communa* and *O. slobodkini* (Georgia, Tall Timbers) and of *O. slobodkini* and *O. notulata* (Tall Timbers/Wakulla Co., Merritt Island NWR, Dixie Co.).[1]

Locus allele	*O. slobodkini* pooled[2]	*O. notulata* pooled[2]	*O. communa* Ga.: Tifton, Thomasville	*O. communa* Tall Timbers, Iamonia, Fla.	*O. slobodkini* Tall Timbers	*O. notulata* Wakulla Co., Fla.	*O. slobodkini* Merritt Is., Fla.	*O. notulata* Merritt Is., Fla.	*O. slobodkini* Dixie Co., Fla.	*O. notulata* Dixie Co., Fla.
GPI	98	81	44	22	33	40	35	30	25	21
4	0.699	0.000	0.011	0.023	0.803	0.000	0.886	0.000	0.940	0.000
5	0.153	1.000	0.932	0.954	0.060	1.000	0.000	1.000	0.000	1.000
IDH1	108	115	44	22	32	54	35	30	25	20
1	0.028	0.000	0.898	0.886	0.000	0.000	0.000	0.000	0.000	0.000
3	0.958	0.996	0.000	0.000	1.000	1.000	1.000	1.000	1.000	1.000
IDH2	88	111	44	21	34	54	35	30	25	20
1	0.006	0.968	0.000	0.000	0.000	1.000	0.000	1.000	0.000	1.000
2	0.000	0.018	0.886	0.809	0.000	0.000	0.000	0.000	0.000	0.000
3	0.989	0.000	0.000	0.000	0.985	0.000	1.000	0.000	1.000	0.000
MDH1	114	90	44	22	34	27	24	23		2
1	0.974	0.954	0.000	0.000	1.000	1.000	1.000	1.000	—	0.750
2	0.026	0.006	0.580	0.500	0.000	0.000	0.000	0.000	—	0.000
5	0.000	0.000	0.420	0.500	0.000	0.000	0.000	0.000	—	0.000
AAT2	112	67	44	22	34	27	24	23	—	2
1	0.036	0.000	0.875	0.820	0.000	0.000	0.000	0.000	—	0.000
4	0.964	1.000	0.125	0.180	1.000	1.000	1.000	1.000	—	1.000
LAP	50	74	21	38	33	27	32	30	24	19
3	0.040	0.426	0.000	0.000	0.000	0.555	0.000	1.000	0.000	0.474
5	0.560	0.486	0.000	0.000	0.727	0.333	0.453	0.000	0.479	0.500
6	0.340	0.007	0.690	0.697	0.258	0.037	0.453	0.000	0.521	0.026
8	0.030	0.007	0.286	0.303	0.015	0.000	0.094	0.000	0.000	0.000

[1] Sample sizes are entered above the frequencies at each locus. Allele frequencies may not sum to one because rarer alleles are not listed. For electrophoretic methods and E.C. designations of enzymes, see Futuyma and McCafferty (1990). Relative mobilities of the electromorphs are as follows. The absolute position (in mm) on a typical gel is given in parentheses for the fastest of the designated electromorphs (relative mobility = 1.00). GPI *4* = 1.00 (73), *5* = 0.95. IDH1 *3* = 1.00 (16), *1* = 0.81. IDH2 *3* = 1.00 (34), *2* = 0.88, *1* = 0.85. MDH1 *5* = 1.00 (26), *1* = 0.88, *2* = 0.77. AAT2 *1* = 1.00 (−20), *4* = 0.65. LAP *3* = 1.00 (65), *5* = 0.91, *6* = 0.85, *8* = 0.78.

[2] Data are from Futuyma and McCafferty (1990), and do not include all the samples listed in the other columns.

on morphological and electrophoretic data, provided evidence that *O. communa* is the sister group of *O. slobodkini* and *O. notulata* taken together (Futuyma and McCafferty, 1990). Because both *O. communa* and *O. slobodkini* feed on *Ambrosia artemisiifolia,* the most parsimonious interpretation of the evolution of host associations in this group is that the association of *O. notulata* with *Iva frutescens* is derived from an ancestral association with *Ambrosia.*

The known geographic distribution of *O. slobodkini* is much more restricted than that of either *O. notulata* or *O. communa.* The major host of *O. notulata, Iva frutescens,* is limited to salt marshes along the Gulf and Atlantic coasts; I have collected this beetle north as far as Long Island, New York, and west as far as Cameron Parish, Louisiana. My only noncoastal record is from Baton Rouge, La., where it was taken on *Iva annua.* Other inland records of *O. notulata* (LeSage, 1986) may represent *O. notulata,* associated with species of *Iva* other than *I. frutescens,* or they may represent *O. slobodkini*; the latter is surely the case for LeSage's records from inland Florida. In peninsular Florida, I have found *O. notulata* on *Iva frutescens* south to Merritt Island on the Atlantic coast and to Crystal River (Citrus Co.) on the Gulf coast. *Ophraella communa* is distributed throughout North America from southern Canada into Mexico, but there are no records from peninsular Florida (LeSage, 1986).

Samples collected from *Ambrosia artemisiifolia,* and conforming to *O. slobodkini* in morphology and allozymes, have been taken from both inland and coastal Florida, from Everglades National Park and Dania in the south to Escambia Co. and Leon Co. (Iamonia) in the north. Eight specimens from Sabine National Wildlife Refuge, Cameron Parish, La., determined electrophoretically as *O. slobodkini,* represent the westernmost record to date. Throughout peninsular Florida, all specimens taken on *Ambrosia artemisiifolia* conform to *O. slobodkini.* This species was found mixed with *O. communa* on *Ambrosia* only in northernmost Florida (*O. slobodkini* comprised 53 of 54 specimens in a collection 19 km west of Pensacola, and about half of a large collection from Tall Timbers Research Station near Iamonia) and in southernmost Georgia (2 *O. slobodkini* and 101 *O. communa* were collected in Thomasville, 29 km northeast of Iamonia). A large collection at Tifton, Ga., 75 km northeast of Thomasville, was composed entirely of *O. communa,* which is also the sole species taken from *Ambrosia* in Athens, Ga., and Baton Rouge, La.

The abruptly complementary distributions of *Ophraella slobodkini* and *O. communa* along the Florida/Georgia border raise the question of whether they are caused by historical or currently acting ecological factors. Many taxa of plants and animals reach their southern or northern range limit in northern Florida, which is also the location of many subspecific boundaries and hybrid zones (Remington, 1968). It has frequently been postulated (e.g., Neill, 1957; Blair, 1965; Remington, 1968) that populations in peninsular Florida differentiated in the Pliocene, when a "Suwannee Strait" may have isolated the region (Frey, 1965), or during the Pleistocene glacial periods, when the biota retreated southward (Deevey, 1949; Auffenberg and Milstead, 1965). Especially during the interglacial periods, a dry corridor along the Gulf coast may have enabled grassland species (including, perhaps, *Ambrosia* and associated insects) to enter Florida from the west (Auffenberg and Milstead, 1965). The palynological record of the late Pleistocene and Holocene indicates that *Ambrosia* and prairie plants were abundant in the dry highlands of central Florida from at least

44,000 years before present (B.P.) until the modern forest began to develop about 4,700 B.P. (Watts, 1980). Along the Florida/Georgia border, a sclerophyllous oak scrub or savanna, probably interspersed with some bluegrass prairie, contained abundant *Ambrosia* from 8,500 to 5,000 B.P., after which a wetter, closed, pine-dominated forest developed, and *Ambrosia* became much less abundant (Watts, 1971, 1980). In the southeastern coastal plain north of Florida, *Ambrosia* pollen is fairly abundant from 29,000 to 9,500 B.P., after which it is much less common (Watts, 1980). *Ambrosia,* possibly harboring populations of *Ophraella,* has therefore long been resident throughout the region. Thus, although latitudinal shifts in vegetation during the several glacial maxima may have provided opportunity for peninsular Floridian populations to become differentiated, *Ambrosia* and associated insects may have been fairly continuously distributed from peninsular Florida to the mainland throughout the late Quaternary, except perhaps in the last several thousand years.

For many reasons, estimates of divergence time based on genetic distances between species (Nei, 1987) are subject to considerable error (Futuyma and McCafferty, 1990). Nevertheless, if we apply Nei's (1987) suggested calibration, the genetic distance between *Ophraella slobodkini* and *O. notulata* (Nei's $D \sim 0.21$) implies divergence about 1.1 million years ago, and that between *O. slobodkini* and *O. communa* ($D \sim 0.35$) about 1.7 million years, i.e., in the early to mid-Pleistocene. There is no direct evidence that *O. slobodkini* differentiated from *O. communa* in peninsular Florida; but even if it did so, there has been ample opportunity, given the historical distribution of *Ambrosia,* for *O. slobodkini* and *O. communa* to penetrate each other's range, unless *O. communa* has spread very recently to eastern North America from the west (its likely region of origin, because the closest relatives of the *O. communa-O. slobodkini-O. notulata* clade have more western distributions: Futuyma and McCafferty, 1990). The considerable uniformity of allele frequencies among populations of *O. communa* and of *O. slobodkini* implies substantial gene flow and vagility. They feed on a plant that at least currently is abundantly distributed across the region of replacement, and which, being an early-successional annual, is often only briefly available in a given site, so that dispersal of the beetles is forced. It is likely that human activities provided openings in which *Ambrosia* could thrive for many centuries before the European settlement (Remington, 1968). Thus current ecological factors are probably responsible for the sharply complementary distributions of these species. Throughout its broad range, *O. communa* occupies its host plant in habitats ranging from mesic to almost xeric; it does not appear highly sensitive to edaphic conditions. This suggests that biological interactions might influence the distributions of these species. In view of the common supposition that competition for resources is rare in folivorous insects (Slobodkin et al., 1967; Schoener, 1983; Connell, 1983; Price, 1983; Strong et al., 1984; but see Faeth, 1988), the possibility that these species' distributions are caused by competitive exclusion is intriguing.

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OVIPOSITION BEHAVIOR OF THE APPLE BLOTCH LEAFMINER, *PHYLLONORYCTER CRATAEGELLA* (CLEMENS) (LEPIDOPTERA: GRACILLARIIDAE)

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Abstract.—Observations of oviposition by apple blotch leafminer moths, *Phyllonorycter crataegella* (Clemens), on apple foliage in the field and in the laboratory indicated oviposition occurred solely on the undersides of leaves, and primarily on the middle third of the leaf (between petiole and apical tip), midway between the mid-vein and margin. A stereotypical sequence of events lasting ca. 1 min was observed prior to egg deposition. This included walking while tapping the leaf underside with the antennae, probing a small area (ca. 1 cm^2) of the leaf with the ovipositor, and violent side-to-side shaking of the abdomen at egg deposition. Results of choice tests in the laboratory suggest apple blotch leafminer moths do not discriminate against oviposition sites previously occupied by freshly deposited conspecific eggs. Our results indicate commercial apple growers may improve control of this pest by applying adulticides just prior to or during the first warm, calm evening in early spring when foliage and leafminer adults are present.

The apple blotch leafminer, *Phyllonorycter crataegella* (Clemens) (ABLM), one of several gracillariid species infesting apple in North America, is distributed throughout much of New England, west to the Hudson River Valley, and south to Virginia (Beckham et al., 1950; Weires et al., 1980; Coli and Prokopy, 1982; Maier, 1983; Van Driesche and Taub, 1983). It parasitizes at least 17 host plants in 7 genera in New England (Maier, 1985). The ABLM completes three generations per year, with the first adults emerging in early spring from pupae in the previous season's leaves. Female ABLM deposit eggs singly on the undersides of host leaves from mid- to late afternoon until dark (Green and Prokopy, 1984). Adult ABLM and larval mines are concentrated in the lower part of apple tree canopies in commercial orchards during the first generation, spreading upwards in succeeding generations (Beckham et al., 1950; Green et al., 1987).

ABLM has achieved major pest status in commercial apple orchards in New York and New England over the past 13 years due to its development of resistance to organophosphate insecticides (Weires, 1977; Weires et al., 1982; Van Driesche et al., 1985). Heavy infestations can cause premature fruit ripening and drop, reduced fruit size and reduced fruit set the following season (Reissig et al., 1982). The oviposition behavior of this insect may have important implications for pest management programs (Green et al., 1987).

Competition for resources could be more important for leaf-mining insects than for species that are more mobile in larval stages (Bultman and Faeth, 1985), as leafminers typically spend their entire larval life within one leaf or portion of a leaf. Intraspecific competition has been demonstrated for other leaf-mining insects (Parel-

la, 1983; Quiring and McNeil, 1984; Potter, 1985), including gracillariid species (Martin, 1956; Bultman and Faeth, 1986).

If competition is important, evolution may favor the development of mechanisms allowing individuals to detect and avoid resources already occupied by conspecifics (Prokopy, 1972; McNeil and Quiring, 1983; Prokopy et al., 1984). Some of these mechanisms may have potential in pest management programs (Prokopy, 1981; Roitberg and Prokopy, 1987).

The objectives of the following study were to describe the oviposition behavior of female ABLM, and examine possible discrimination against host leaves previously occupied by conspecific eggs.

MATERIALS AND METHODS

All observations of ABLM oviposition in the field (experiment 1) were conducted in commercial apple orchards in New England during 1983 and 1984, as part of a larger study of ABLM behavior (Green and Prokopy, unpubl. data). An area within the canopy of an apple tree was selected at random, and the undersides of leaves were searched until an ABLM adult was located. The activity of the moth was recorded for 5 min, or until the moth flew out of sight of the observer. We recorded the number of ovipositions, leaves visited, repeat visits to the same leaf, and whether a moth arrived on a leaf by flight or by walking.

ABLM observed in the laboratory (experiments 2, 3, 4) were collected as pupae in leaves from commercial apple orchards in western Massachusetts. The portions of leaves containing mines were held individually in 30 ml plastic cups until adult emergence. Upon emergence, males and females were placed collectively in a 3.8 l glass jar, the opening of which was covered with organdy cloth to permit air circulation. Each morning, mating pairs were removed from the jar and placed in the cups until females were used for experimentation the following day. Throughout, ABLM adults were provided free access to spring-water-soaked dental wicks, and maintained under natural lighting in front of a large screened window. All laboratory experiments, conducted on a table placed in front of this window, occurred from 1600–2100 hours (Eastern Standard Time), the time of peak ABLM oviposition in the field (Green and Prokopy, unpubl. data).

Foliage used in laboratory experiments was collected daily from unsprayed apple trees and carefully examined to exclude leaves with leafminer eggs or larval mines. Only basal leaves (or fruit cluster leaves, experiment 4) of growing terminals were selected for use in the choice tests to provide uniform leaf age and quality. Leaves were maintained on the terminals, held in water-filled vials. Average leaf size in experiments 2 and 3 was 6.2 by 4.2 cm.

During the summer of 1984, 23 ABLM were observed individually in the laboratory for 3 hr each (experiment 2). Each moth was held in a vertical cylindrical cage of clear acetate (14 cm diameter, 25 cm height), containing an apple terminal with 8 leaves. The base of the terminal extended through a hole in the floor of the cage (a plastic petri dish bottom) into a vial containing water. The top of the cage was covered with organdy cloth to allow air circulation. ABLM females were placed singly in a stoppered vial within the cage, and were allowed to acclimate for 5 min before the cotton stopper was removed (remotely, by pulling a string) and observations were

begun. The number and sequence of leaf visits, number and location of ovipositions, and the sequence of behaviors involved in oviposition were timed and recorded. After 3 hours, the moth was removed from the cage. The number of ovipositions was confirmed by examination of leaves under a microscope, and the length and width of each leaf was measured and recorded. The location of the first egg only (to eliminate any influence of previous ovipositions) on each leaf was plotted according to distance from petiole, margin, and midrib.

In experiment 3, conducted during the summer of 1984, individual ABLM females (caged as in experiment 2) were provided with a terminal of 2 leaves, one containing 1 or 8 ABLM eggs (oviposited <30 hr previously) and one without prior ovipositions (=clean). Each female was observed 30 min or until the first oviposition. Each female was pre-tested by being allowed to oviposit freely on a clean leaf until it left the leaf. Only females which oviposited at least once in the pretest were used in the experiment.

In experiment 4, conducted in July of 1987, individually-caged ABLM females were provided with 2 small leaves (average size 2.3 by 1.4 cm), one clean and one with 1 or 2 prior ovipositions. The leaf half (right or left of the midvein) containing or receiving eggs was noted. ABLM females were pre-tested by being offered 3 pairs of clean leaves in succession, the next pair being offered after one oviposition. Only females which oviposited three times prior to the assay were used.

RESULTS

In commercial apple orchards, 25 ABLM females were observed exhibiting oviposition behavior (Table 1), all between 1645 and 2035 hours. Of the 25, 8 moths were observed probing the leaf underside with the ovipositor but did not oviposit while under observation. All ovipositions occurred on the undersides of leaves, though arrival was on the upper surface of leaves in about half of all visits (N = 102 total visits). Overall, 19.1% of leaves visited received an egg, and 8.8% of all leaf visits were repeat visits by the same female to the same leaf. No moths oviposited more than once per leaf visit. In one instance a second egg was placed on a leaf previously oviposited on by the same female during a prior visit. About two-thirds of leaf visits were via walking from the stem or adjacent leaves (Table 1), and about one-third were by flight.

Repeated attempts to observe oviposition in the laboratory under artificial lighting were unsuccessful, although females confined for several days with foliage under those conditions did eventually oviposit. We succeeded in observing oviposition by offering foliage to females in front of a screened window, under natural lighting, temperature, and humidity, and during the time period within which oviposition occurs in the field.

Of the 23 moths observed in the laboratory for 3 hr, 19 visited foliage and 15 oviposited at least once, for an overall average of 6.7 eggs per female (range = 0–20). After tarsal contact with a leaf, females spent an average of 30 s (±3.1 s, SE) walking on the leaf, during which they continuously tapped the leaf surface with the antennae, gradually narrowing down the area "searched" by walking in an increasingly tighter circle. Once ovipositor contact with the leaf occurred, females spent an average of 29 s (±3.4 s) probing a small area of the leaf (ca. <1 cm^2) with the ovipositor, often taking short, backward steps. This period ended with the abdomen bent at a

Table 1. Observations of ABLM exhibiting oviposition behavior (=ovipositor in contact with leaf) in commercial apple orchards in New England, 1983–1984.[a]

	Mean per moth (±SE)
Minutes observed	3.7 ± 0.69
Number leaf visits	4.1 ± 0.52
Number different leaves visited	3.8 ± 0.47
Number ovipositions observed	0.8 ± 0.62
	Proportion ± SE
Proportion leaves visited	
By walking	69.6 ± 0.01
By flight	30.4 ± 0.01

[a] Twenty-five moths were observed individually for 5 min or until leaving sight of observer. Data include 9, 12 and 4 ABLM during first through third generations, respectively.

near 90° angle to the rest of the body and the ovipositor firmly planted against the underside of the leaf. The female then shook violently 3–5 times from side to side, for a total of about 1 s, after which time the egg was deposited on the leaf surface. The moth then quickly lifted the abdomen and ovipositor off the leaf surface, and crawled away from the egg an average of 13.1 s (±3.4 s) after the ovipositor was firmly in place on the leaf underside.

On the first leaf visit by laboratory-observed moths, females frequently oviposited more than once before leaving (mean 1.7 eggs/first leaf visit/female). They did so much less frequently on subsequent leaf visits (mean 0.7 eggs/leaf visit/female). Among the 15 replicates in which oviposition occurred, 78% of leaf visits did not result in an oviposition.

Females oviposited significantly more eggs ($P < 0.5$, G-test, Sokal and Rohlf, 1981) on the middle of three lateral sections of the leaf (sectioned perpendicular to mid-vein, Fig. 1a), and the second and third quarters longitudinally (sectioned parallel to mid-vein, Fig. 1b). Among the 8 leaves on each terminal, no preference was exhibited for any particular leaf position relative to the most basal or apical leaf.

In experiment 3, no significant differences were detected in the number of new ovipositions on clean leaves vs. leaves with one (N = 26) or eight prior ovipositions (N = 29), although substantially more new eggs were placed on clean leaves vs. leaves with 8 prior ovipositions (19 vs. 10, respectively). ABLM females oviposited on the first leaf visited (53 of 55 replicates, or 96%), regardless of the presence or absence of prior ovipositions. For some unknown reason, ABLM females were not nearly as selective as they were in the field or in experiment 2, where only 19% and 32% of leaf visits resulted in oviposition, respectively.

Resolving these concerns was the rationale for the final experiment, in which small leaves were used and the leaf-half receiving the new egg was noted (Table 2). By restricting the amount of leaf area available and comparing oviposition on the basis of a portion of the leaf, discrimination by females against small occupied areas of the leaf might become apparent. Pretesting each female on 3 clean leaves (vs. only 1 in experiment 3) was intended to accentuate "choosiness" by reducing any effect of oviposition deprivation and by providing uniform pre-assay oviposition experience which could be necessary for recognition of conspecific eggs or host markers.

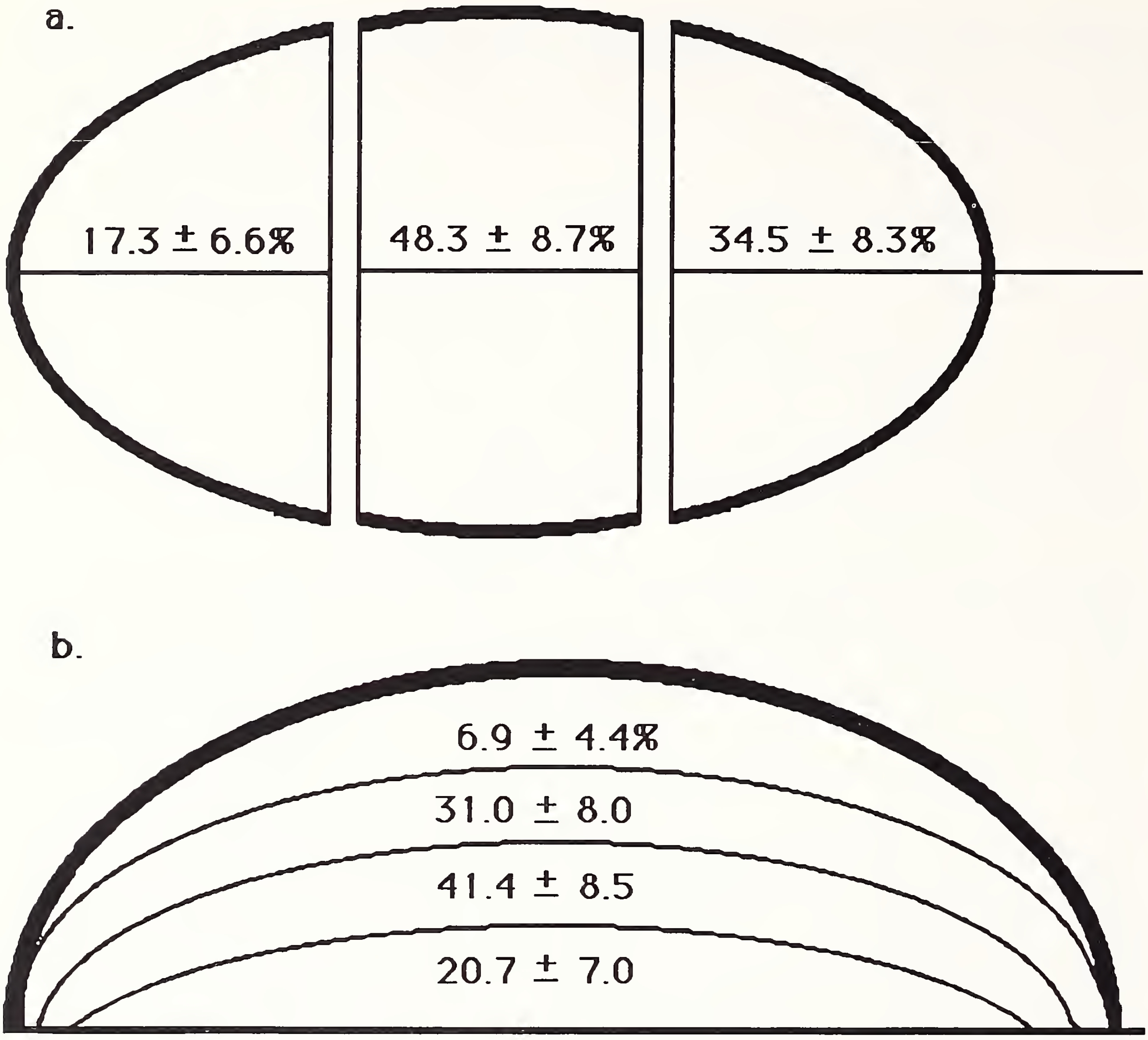

Fig. 1. Lateral (a) and longitudinal (b) distribution of ABLM eggs according to leaf surface area ±SE. Eggs deposited during 3 hr observations in laboratory. Only the first egg deposited on any leaf was included, N = 58 eggs, 15 moths.

"Choosiness" was greater in this experiment (56% of leaf visits resulted in an oviposition) than in experiment 3, but still not equal to levels observed in orchards or in experiment 2. The first leaf visited received the first oviposition in 56% of all replicates.

No discrimination was detected against entire leaves or leaf halves containing one or two previous ovipositions. Leaves with one prior oviposition received new eggs as often as did clean leaves (Table 2). Of the 14 new eggs placed on leaves with a prior oviposition, 7 were placed on the same half (right or left side of the mid-vein) of the leaf underside as the initial egg. Leaves with 2 prior ovipositions received significantly more new eggs than did clean leaves.

DISCUSSION

Results of this study agree with observations by Beckham et al. (1950) of a concentration of oviposition by ABLM on the mid-section of the leaf. Pottinger and

Table 2. Comparison of oviposition by individually caged ABLM females provided with 2 leaves, one free of conspecific eggs (=clean) and one with 1 or 2 ABLM eggs deposited <30 hr previously. For leaves with prior oviposition, comparison is between halves of leaves (leaf divided by the midvein) receiving the new egg.

Treatment	N	Leaf receiving new egg[a]	
		With egg(s)	Clean
1 previous egg	28	14a	14a
2 previous eggs	13	11a	2b
		Leaf half receiving new egg	
		Half with egg(s)	Clean half
1 previous egg	14	7a	7a
2 previous eggs	7	5a	2a

[a] First egg on leaf only. ABLM were allowed a single oviposition on each of 3 clean leaves <30 min prior to testing. Data within a row and followed by the same letter are not significantly different ($P > 0.05$, *G*-test, Sokal and Rohlf 1981).

LeRoux (1971) found no preference for the proximal or distal leaf half in a related species, the spotted tentiform leafminer (STLM), *P. blancardella* (F.), but they did not report distribution by thirds as presented here. Otherwise, their description of oviposition behavior is similar to what we observed in ABLM. They speculated that the violent side-to-side shaking by females immediately prior to egg deposition might clear the leaf surface and/or ready the egg for deposition.

The extent and importance of inter- and intraspecific competition in regulating natural populations has been a topic of considerable interest in the recent literature (Lawton and Strong, 1981; Schoener, 1982, 1983). Intraspecific competition for larval resources is unlikely in leafminer populations maintained at low densities by natural enemies (Faeth and Simberloff, 1981). Regulation of ABLM population densities by parasites has been noted by many workers (Dean, 1940; Gambino and Sullivan, 1982; Maier, 1982; Van Driesche and Taub, 1983; Van Driesche et al., 1985; Drummond et al., 1985). However, competition might occur, even at low ABLM densities, if the supply of superior leaves or portions of leaves is limiting.

As in most but not all lepidopteran leafminers (Gross, 1986), the ABLM is restricted for its entire larval life to one portion of a leaf (larvae do not cross major leaf veins), chosen by the female adult. Results of this and previous studies indicate ABLM females oviposit preferentially on the mid-section of leaves, within the interior half of the tree canopy throughout the season, and in the lower portion of the canopy during the first generation (Beckham et al., 1950; Green and Prokopy, unpubl. data). This part of the canopy may be preferred due to less wind interference with oviposition, closer proximity to emergence sites (Beckham et al., 1950), or a reduced tendency for interior leaves to abscise prior to completion of larval development (Bultman and Faeth, 1986b).

Other factors that might limit availability of favorable oviposition sites include the lesser amount of apple foliage in early spring and proximity to shelter (Martin, 1956). Selection of leaves by leafminers according to leaf size (Bultman and Faeth, 1986a), nutrient content, or exposure to the sun (Faeth et al., 1981), or selection against leaf noxious compounds or damaged leaves (Faeth, 1985) may also occur.

The "choosiness" of ABLM noted here (i.e., visiting many leaves without ovipositing, Table 1), suggests that these or other factors may operate in ABLM oviposition site selection.

Restricted availability of superior oviposition sites may lead to over-utilization of existing sites. Interference competition among larvae, including cannibalism, has been demonstrated in other gracillariids, including STLM (Pottinger and LeRoux, 1971) and the aspen blotch leafminer, *P. salicifoliella* (Chambers) (Martin, 1956), and in the dipteran leafminers *Agromyza frontella* (Rondani) (Quiring and McNeil, 1984) and *Liriomyza trifolii* (Burgess) (Parrella, 1983). Interference competition without cannibalism has been observed in another dipteran, the native holly leafminer, *Phytomyza ilicicola* Loew (Potter, 1985). Besides cannibalism, the presence of conspecifics may also result in a general depletion of resources, leaf abcission, or in induction of plant defenses.

Possible restricted availability of favorable oviposition sites, limited mobility of ABLM larvae and adults (Beckham et al., 1950; Green and Prokopy, 1986), and relatively permanent host plants (present over 3 generations) are ecological characteristics which have been positively correlated with host marking ability, used to avoid reduced fitness or mortality due to overcrowding in other species (Prokopy, 1981; Roitberg and Prokopy, 1982, 1987). The broad host range of ABLM (17 species, Maier, 1985) is one characteristic not generally found in species which mark hosts. Given the concentrated searching behavior by ABLM prior to oviposition coupled with the presence of ABLM eggs on the surface of the leaf (as opposed to eggs inserted internally), host marking may not be required for ABLM to recognize previously occupied sites. Energetic costs and potential costs due to use of host-marking cues by natural enemies may outweigh any benefits (Roitberg and Prokopy, 1987).

Oviposition twice on the same leaf by a single female in the field (experiment 1), lack of discrimination by ABLM females against leaves with one egg (experiment 3), concentrated "searching" behavior over a small leaf area prior to oviposition in the lab (experiment 2) and the ability of a single apple leaf to support several ABLM larvae (Reissig et al., 1982) suggest that the biologically significant unit chosen for egg laying by a female may be a portion of the leaf rather than the entire leaf. The substantially though not significantly greater new oviposition on clean leaves vs. leaves with 8 prior ovipositions (experiment 3) suggested possible discrimination on the basis of prior egg density. However, in all but 2 of the replicates, the first leaf visited received the first oviposition. Any discrimination against the leaves with 8 prior ovipositions would have been on the basis of cues other than contact with the leaf or eggs.

The significant preference for leaves with 2 prior ovipositions suggests that some other factors, possibly related to leaf quality per se, may be more important in ABLM selection of leaves for egg laying than the presence of conspecific eggs, or that clumping of eggs may be advantageous. Alternative hypotheses for the apparent failure of ABLM females to discriminate against previously egg-occupied host leaves or parts of host leaves include (1) reduced "choosiness" in this assay; (2) discrimination only at egg densities greater than those tested, or only against sites occupied by larvae or by eggs that are more mature; (3) a conspecific egg recognition/discrimination system may not have developed in ABLM because of insufficient selection pressure for such a system.

ABLM mate at temperatures at least as low as 7°C (Green and Prokopy, unpubl. data), but oviposition by ABLM and STLM may be restricted to periods of higher temperature (>9–15°C) and low wind speeds (Trimble, 1986; Green and Prokopy, unpubl. data). Therefore, a considerable buildup of mated female ABLM in sheltered locations may be possible until conditions are appropriate for oviposition. Once these conditions occur, ABLM females are capable of ovipositing up to 20 eggs each (average = 6.7 eggs per female) during a single 3-hr period. Thus, when needed, orchardists should apply adulticides against ABLM just prior to or during the first warm (>9–12°C), calm evening in the spring when foliage and ABLM adults are present.

Aspects needing additional work include examination of the distribution of ABLM eggs and larvae in the field for clumped, random or uniform dispersion, density dependent effects on larvae occurring from presence of conspecifics on the same leaf or different leaves on the same tree, and possible discrimination by ovipositing adults against leaves or portions of leaves occupied by larvae or by more mature conspecific eggs.

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BIOLOGY AND IMMATURE STAGES OF *CHLOROPS CERTIMUS* AND *EPICHLOROPS EXILIS* (DIPTERA: CHLOROPIDAE), STEM-BORERS OF WETLAND SEDGES

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Abstract.—The life cycles of *Chlorops certimus* and *Epichlorops exilis* are described and illustrated. The adults are found in freshwater marshes where their host plants, species of the sedge genus *Carex,* occur. Eggs are deposited on the sheathing leaves of the host, and the larvae are stem borers. Both species are univoltine, overwintering as nearly mature larvae near the base of the sedge culm. Puparia are formed within the culm, and adults emerge in northeastern Ohio in early to mid-June.

The family Chloropidae, containing about 1,300 species in the world, is one of the more intriguing and colorful members of the cyclorrhaphous Diptera. Some 270 species and 55 genera have been recorded from the Nearctic Region (Sabrosky, 1987). Phylogenetically, the Chloropidae are placed in the superfamily Ephydroidea, a sizeable taxon that includes 9 families of Acalyptratae (McAlpine et al., 1981).

The Chloropidae is one of the four major families of Diptera that have largely phytophagous larvae (Oldroyd, 1964), being associated particularly with grasses, sedges, and rushes. A few of the plant-feeding forms, such as the frit fly (*Oscinella frit* [L.]) and the wheat stem maggot (*Meromyza americana* Fitch), have become economically important pests of cereals and pasture grasses. In addition to the numerous phytophagous species, there are a fair number of chloropid taxa that have saprophagous larvae and even a few that are predaceous (Oldroyd, 1964; Ferrar, 1987; Sabrosky, 1987). Many of the scavenger species are secondary invaders of plant tissue that has been damaged by the feeding of other insect larvae (Valley et al., 1969). A few species of Chloropidae are of some medical significance. For example, eye gnats of the genus *Liohippelates* (formerly *Hippelates*) are suspected to be vectors of various eye disorders and yaws (Herms, 1928).

Most research on the biology of the family has been restricted to species having agricultural or medical significance, although most chloropids are not thought to be economically important. A few species of *Chlorops, Eribolus, Elachiptera,* and *Oscinella* have been reported to be primary or secondary invaders of stems of wetland monocots belonging to the sedge family Cyperaceae (Valley et al., 1969).

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This paper includes life history data for *Chlorops certimus* Adams and *Epichlorops exilis* (Coquillett), two stem-boring species that attack sedges belonging to the genus *Carex*. The eggs, 3 larval instars, and puparia for both species are described and illustrated.

MATERIALS AND METHODS

Collecting Techniques

Adults were obtained by sweeping herbaceous vegetation in marshy habitats occurring in northeastern Ohio. Captured adults were aspirated alive into 8-dram shell vials and transported to the laboratory where they were placed in breeding chambers. The latter consisted of baby food jars (5 × 7 cm) which had their bottoms removed. A piece of fine mesh nylon was placed over the mouth of the jar and held in place by a rubber band. The open end of the jar was then placed in a petri dish that contained a substrate of moist peat moss. A small pellet of a mixture of honey and brewers' yeast, for adult feeding, was pressed against the upper side of the glass wall. Freshly cut stem sections of potential host plants were placed vertically into the peat moss to provide resting and oviposition sites. Stems were replaced every 2 days. The breeding containers were inspected daily for adult behavior and oviposition.

When eggs were observed, they were carefully removed with a fine camel's hair brush, counted, measured, and placed in small petri dishes containing a piece of moist filter paper. A portion of the leaf blade was also included as substrate. Newly hatched larvae were either set up for life cycle studies or preserved for illustration purposes.

Larval stages were collected in nature by examining potential host plants belonging to the Cyperaceae and other monocot families occurring in the study area. Roots, stems, and inflorescences of suspected host plants were dissected and examined in the field. Immature stages were transferred, along with a portion of the host plant, to an 8-dram shell vial, corked, and held for further investigation. Additional host plants were uprooted, placed in large plastic bags, and taken to the laboratory.

Plants brought back to the laboratory were slit open, and data concerning instar, feeding habits, and position of larvae recorded. Larvae were then transferred to fresh stems and placed in 8-dram shell vials which, in turn, were put into a beaker measuring 9 × 9.5 cm. The beakers (containing as many as six vials) were put into plastic bags (to maintain proper humidity) and placed in a long-day photochamber (16L: 8D) set to promote maximum freshness of the stems (ca. 20°C) without interfering with larval development. Infested stems were checked every 2 days for information concerning feeding habits and duration of larval stadia.

Recently formed puparia were maintained in the sedge culms which were cut into 4 cm lengths and held on moist peat moss in petri dishes. Daily observations provided information on the duration of the prepupal and pupal periods and emergence times of the adults.

Preservation and Preparation of Specimens

Eggs were preserved in ¼ dram vials containing KAAD, plugged with cotton, and stored in 8-dram vials containing 80% ethanol. Larvae were killed either by dropping them in boiling water or by placing them into a stender dish containing KAAD

solution. They were stored in 80% ethanol. Gross morphology was studied by placing eggs and larvae in a small stender dish containing 80% ethanol.

To study minute morphological structures, larvae were dissected with iridectomy scissors, the soft parts being teased away with sharpened minuten pins embedded in the tips of wooden match sticks. Taxonomically important structures (cephalopharyngeal skeletons and anterior and posterior spiracles) were dissected out of the larvae and/or cast exuviae whenever possible. These structures were transferred to microscope slides containing a drop of glycerine and stored in large petri dishes. Occasionally the first and last three segments of the third-instar larvae were dissected away and cleared in hot NaOH or KOH for 5 minutes, after which they were transferred to a depression slide containing a drop of glycerine, and stored in petri dishes.

Puparia were killed in KAAD, measured, and then preserved in 80% ethanol. Puparia that produced adults were placed in #5 gelatin capsules and pinned below the reared adult.

BIOLOGICAL OBSERVATIONS

Chlorops certimus

Chlorops, the largest genus of the subfamily Chloropinae, consists of some 35 species in North America (Sabrosky, 1987). Most species are small and yellow with black or reddish brown mesonotal stripes. Individual species are rarely taken in large numbers and are usually obtained by sweeping wetland herbaceous vegetation.

Most of the life history information for the genus has been restricted to the economically important Palearctic species *Chlorops pumilionis* (Bjerkander). Often called the gout-fly of barley and wheat, this species is responsible for considerable damage to cereal and grain crops throughout Europe (Frew, 1923a, b; Oldroyd, 1964). Its larval stages have been described in great detail by Frew (1923a, b), Goodliffe (1939, 1942), Lilly (1948), Nye (1958), and Dennis (1961).

Larvae of other species of *Chlorops* have also been reported to be primary invaders of grasses and sedges (Wendt, 1968; Zhabinskaya, 1963). *Chlorops obscuricornis* Loew was reared from the spike rush *Eleocharis smallii* Britt. (Valley et al., 1969), and d'Aguilar (1943) reared *C. frontosa* Meigen from the stem of an unidentified species of *Carex.*

Chlorops certimus is a rather common, widely distributed, and highly variable species. It has been recorded from Quebec and Massachusetts west through Ohio, Indiana, and Illinois to Alaska and south to North Carolina, Texas, and Utah (Sabrosky, 1965).

All rearings were initiated from larvae and puparia collected in the culms of *Carex lurida* Wahlenb. or from adults collected in sedge marshes. Larvae of *Chlorops certimus* have also been reported as primary invaders of *Carex hystricina* Muhl. and *C. pennsylvanica* Lam. (Valley et al., 1969).

Adults emerged in nature between late June and late July and remained relatively abundant until mid-August, after which their numbers declined rapidly. The earliest record for captured adults was June 24; the latest, September 29. Males reared from puparia lived 16–21 days; females, 20–33 days. Generally, males emerged first followed in a few days by females.

Field collected and reared adults were kept in rearing chambers along with a portion

of their host plant. In most cases, both sexes remained intimately associated with the provided vegetation, usually resting head downward about one-half to three quarters of the way up the stem. Adults spent very little time on the peat moss, visiting it only to obtain moisture. On many occasions, both males and females were observed grooming themselves on the sides of the rearing chamber and the nylon netting. The front tarsi were used to clean the anterior thoracic and head bristles, and the middle and hind tarsi were repeatedly rubbed over the partially spread wings.

The premating period for laboratory-reared adults was 18–24 hr. On one occasion, a male was seen mating 6–8 hr after emerging with a female that had emerged one day earlier. No overt courtship behavior was noticed. Prior to mating, a male flew to where a female was resting, walked up to her, and when directly in front of her, flew or leaped onto her dorsum. If the female was non-receptive, she immediately decamped by flying or walking away. If the male was aggressive and persisted in his efforts to mount a non-receptive female, she pushed him away by flicking her wings.

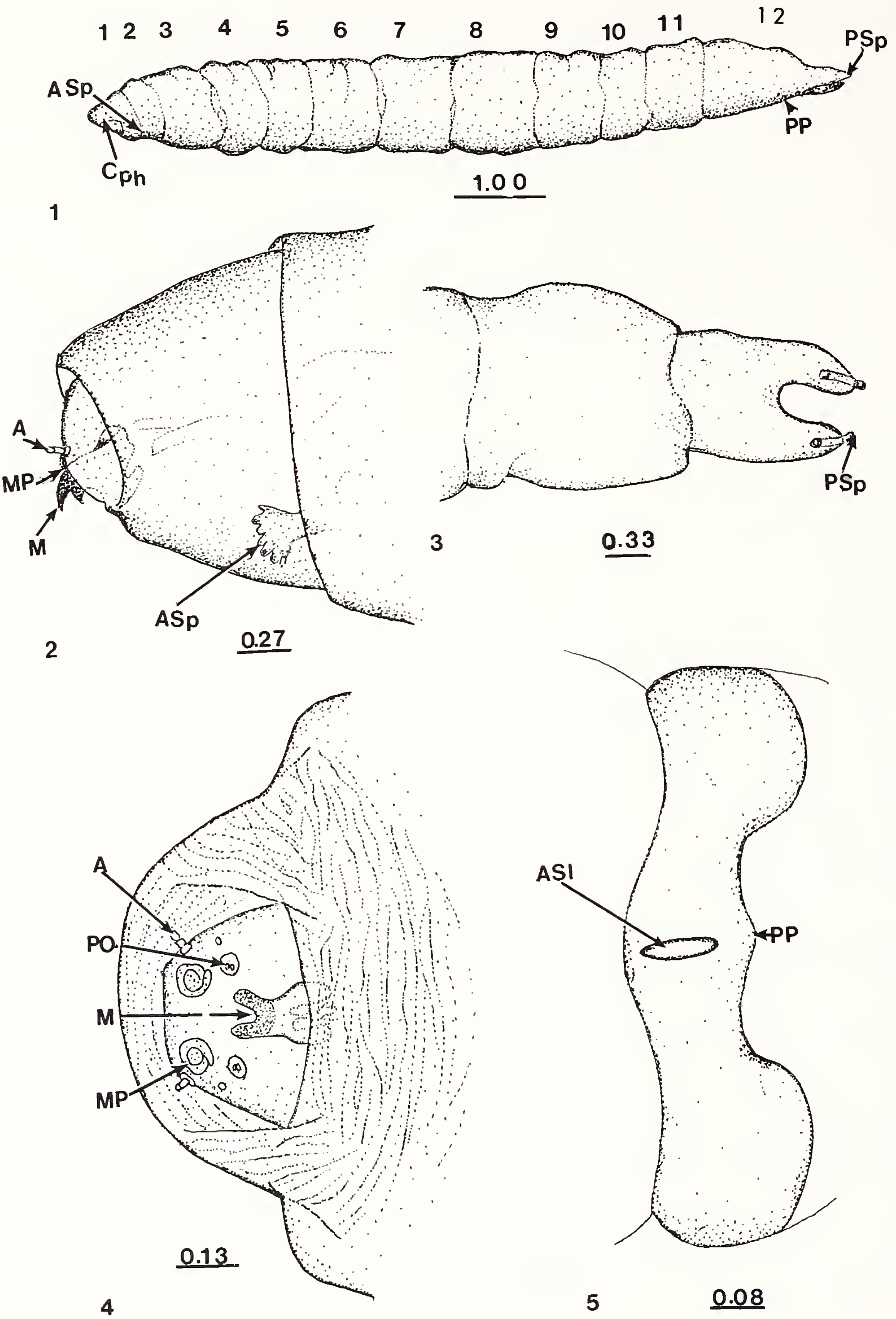
Mating was almost a daily occurrence, and individual pairs often were seen mating as many as three times per day. The average time spent in copula was 35–45 minutes. Mating was observed most frequently during the afternoon and/or early evening hours. Field collected adults usually mated within 10 minutes after being transferred to the plastic rearing chambers.

In copula, the male positioned himself dorsad the female and almost parallel to her body. His head was directly above her scutellum, and his wings were folded flat over his abdomen. The male's fore tarsi were placed on the female's wing bases, and the middle tarsi were appressed against the sides of the female's abdomen approximately one-third of the way back. The hind tarsi of the male were locked around the posterior end of the female's abdomen forming an "X" when viewed from below. The female usually was quite active while in copula. If not walking about the sides of the container, she was usually feeding or grooming her head region with her fore tarsi. At the termination of coitus, the male simply walked off anteriorly.

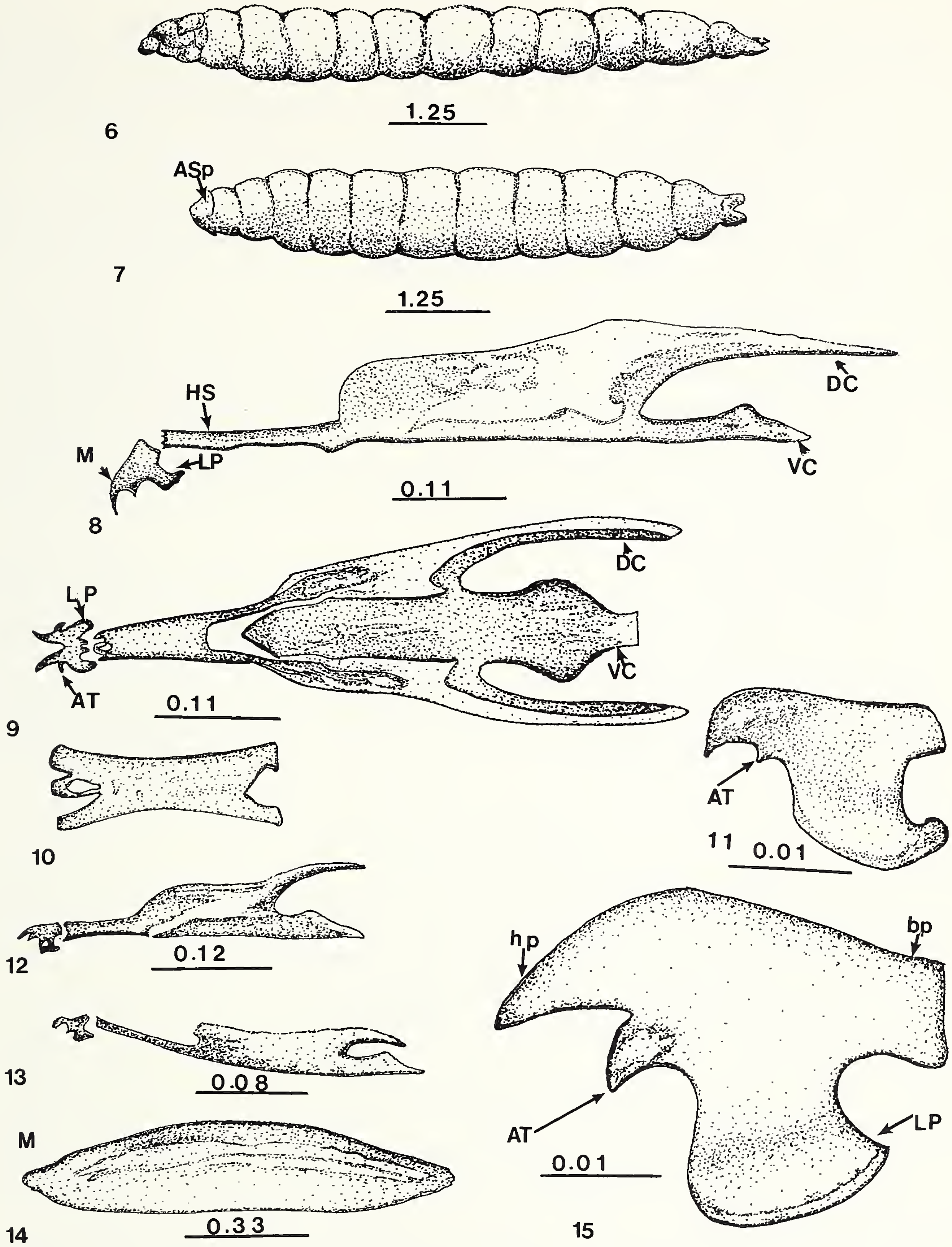
The preoviposition period (from emergence of the female to her first oviposition) lasted 8–14 days. In nature, eggs were found singly on the upper sides of the leaves usually close to the ligule of the host plant. At other times, eggs were found near the tip of the leaf. A few eggs were cemented to the leaf surface between two adjacent longitudinal veins. In the laboratory, field collected and reared females simply deposited eggs on any portion of the vegetation provided as well as on the sides of the rearing chamber and nylon netting.

Two isolated females deposited 65 to 80 eggs, respectively, over a 10–12 day period. The incubation period was 6–7 days. Newly hatched larvae in petri dishes immediately crawled beneath the moist paper toweling. These were transferred to young culms of *Carex lurida* measuring 15–18 cm in height. First instars were very difficult to maintain as they would feed only on fresh stem tissues.

Egg remnants found in nature indicated that newly hatched larvae were oriented with their heads toward the leaf apex. Therefore, larvae must reverse direction and make their way to the ligule and eventually between the overlapping edges of the sheathing leaves. After entering the culm, larvae descended while feeding along the edges of the inner leaves. As larvae moved down the leaf blade, they passed between the successive inner sheaths until they reached the center of the shoot. Repeated observations revealed that larvae bored directly through one or more of the inner



Figs. 1–5. *Epichlorops exilis*, third instar. 1. Lateral habitus. 2. Lateral view of cephalic segment. 3. Dorsal view of posterior end. 4. Ventral view of anterior end showing facial mask. 5. Perianal pad.



Figs. 6–15. *Epichlorops exilis*. 6. Puparium, lateral habitus. 7. Same, dorsal habitus. 8. Third instar, lateral view of cephalopharyngeal skeleton. 9. Same, dorsal view. 10. Same, dorsal view of hypopharyngeal sclerite. 11. Second instar, lateral view of mandible. 12. Same, lateral view of cephalopharyngeal skeleton. 13. First instar, same. 14. Eggs. 15. Third instar, lateral view of mandible.

leaves to reach the center of the culm. Once at the center, the first instars continued to feed as primary invaders on the developing peduncle and tender portions of the innermost leaves. Feeding by the second instars eventually severed the peduncle, thus preventing the inflorescence from growing out of the sheath. The second and third instars then continued to feed on the immature inflorescences and on the peduncle, usually destroying most of the tissues enclosed within the sheath.

In nature, usually one and occasionally two larvae were found per stem. In all cases, they seemingly fed by rupturing individual cells with their highly sclerotized mouthhooks and then sucking up the exuding cellular protoplasm along with structural components of the ruptured cells.

The first larval stadium lasted 24–36 hours; the second, 7 to 10 weeks; and the third, 38–40 weeks. The mature third instar, which usually faced downward, reversed position a short time prior to pupation and migrated a short distance up the stem. Pupation occurred about 1.5 cm below the ligule of the leaf blade. On several occasions, the third instar pupated under the outermost sheathing leaf blades approximately 5–10 cm above ground level. The prepupal period lasted 3–3.5 days; the pupal period, 10–11 days for both sexes.

In northeastern Ohio, *C. certimus* was univoltine, with adults emerging in late June. Eggs were deposited during late June and early July, and larvae became abundant in stands of *Carex lurida* in early to mid-July. Overwintering occurred as larvae in a state of temperature-controlled quiescence; second and third instars collected in November and December began to feed actively when brought into the laboratory, pupated, and eventually emerged as adults. Puparia were encountered in nature between late May and early June.

Epichlorops exilis

The genus *Epichlorops* is represented in North America by only three species. *Epichlorops puncticollis* (Zetterstedt) is Holarctic in distribution, whereas *E. exilis* (Coquillett) and *E. scaber* are strictly Nearctic. The taxonomy of the genus is relatively well understood, but information on the biology and immature stages is lacking.

Morphologically, the genus *Epichlorops* appears to be closely allied to the genera *Chlorops* Meigen and *Cetema* Hendel (Becker, 1910). However, adults of *Epichlorops* are easily recognized in that they are conspicuously large and have a characteristically yellow and black body. In addition, the dorsum of the thorax is uniformly black, without the longitudinal stripes that are characteristic of *Chlorops.* Also in contrast to *Chlorops,* the dorsum of the thorax is strongly punctate, a condition similar to that found in *Cetema.*

Epichlorops exilis is an attractive, moderately large fly measuring 4–5 mm in length. Adults are easily recognized by the yellow head that bears a conspicuously shiny black ocellar triangle, the black abdomen with the sides and venter yellow, the uniformly black body and coarsely punctured mesonotum, and by the yellow scutellum. The species ranges from Massachusetts to Washington and Saskatchewan, and south to Ohio and Iowa (Sabrosky, 1965).

Biological observations are based on rearings initiated from larvae and puparia found in stems of *Carex crinita* Lam. and from adults collected in sedge marshes.

Adults were abundant in moist, partially shaded regions of marshes, particularly

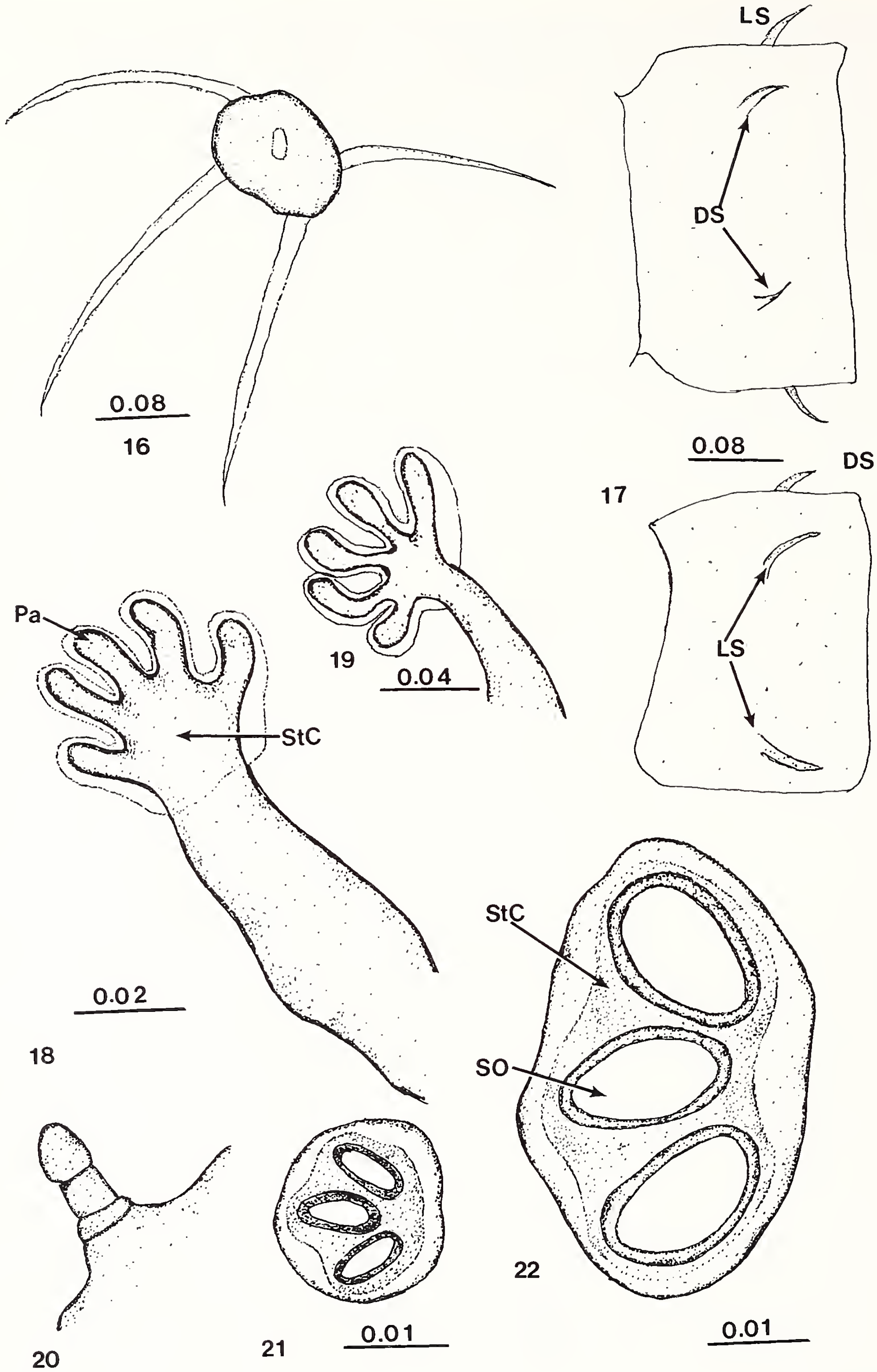
in the early morning hours. They showed fidelity to their host plants, and only a few specimens were taken in adjacent stands of wetland monocots. In a marsh near Kent, adults were abundant in a stand of *Carex lacustris* Willd.; occasional in reed canary grass, *Phalaris arundinacea* L. (a few plants of *C. lacutris* occurred in this stand); and very rare in *Carex stricta* Lam. (Fig. 42). Both males and females were often observed resting on stems with their heads facing downwards. They were usually seen about three quarters of the way up the stems of their host plant, or horizontally on the dorsal surfaces of the leaf blades near the ligule of the culm. On several early morning collecting trips, males and females were often observed extending and retracting their proboscis into and out of drops of dew that had collected the night before on the leaf blades and stems.

In the laboratory, adults of *E. exilis* were confined to rearing chambers and provided with a portion of a stem of *C. crinita* measuring 10 cm in length. Both sexes spent much time on the stems, usually walking up and down the sheathing leaves. On several occasions females were observed near the ligule of the stem, oriented towards the apical end of the leaf blades. This is the normal ovipositing position. When not ovipositing, they were observed grooming themselves with their front tarsi. When on the sides of the jar, they appeared to walk side ways. They always remained in close proximity to each other. However, if surprised or frightened by sudden movement of the light or jarring of the table, both sexes quickly retired to the vegetation or peat moss. Frequently they were seen mating while upside down on the cloth netting that covered the mouth of the breeding jar.

Gravid females collected in nature lived from 10–14 days in the laboratory; males, 10–12 days. If reared from larvae or puparia, males lived from 25–30 days; females, from 29–30 days. Sexual dimorphism was evident, as females were distinctly larger.

In the laboratory adults were frequently observed feeding on the fly food. In most cases, water was obtained from droplets that collected on the vegetation from daily watering or from the moistened peat moss. If the peat moss was too moist, adults frequently became trapped and were often found dead the next morning. Grooming activity usually centered about the head and wings. The front tarsi were used to clean the head bristles and antennal regions, and the middle tarsi were used to groom the wings and mid-section of the abdomen. The posterior part of the abdomen was cleaned with the last pair of tarsi.

Mating was observed in nature commonly in the early morning hours, usually between 8:30 and 10:30 AM, and in the evening. In the laboratory, mating occurred repeatedly with no obvious preference as to time of day. In general, mating took place shortly after adult emergence. The premating period averaged between 16 and 24 hours, the time probably required for partial sclerotization of the exoskeleton and complete body pigmentation. No overt courtship behavior was observed, although the male periodically was seen presenting himself to the female by walking up to and then standing directly in front of her. Non-receptive females would turn around and walk away or fly to the side of the rearing chamber. If a male attempted to mount a non-receptive female, she would dislodge him by simply flicking her wings. A receptive female remained relatively motionless for a moment and then, after a short period of grooming, extended her wings laterally away from her body (about 40–45°). The male then either walked around her and mounted posteriorly or simply flew onto her back. Both procedures were observed on several occasions.



Figs. 16–22. *Epichlorops exilis.* 16. First instar, posterior spiracular plate. 17 (top). Same, dorsal view of fifth abdominal segment showing spines. 17 (bottom). Same, lateral view. 18. Third instar, anterior spiracle. 19. Second instar, same. 20. Third instar, antenna. 21. Second instar, posterior spiracular plate. 22. Third instar, same.

Females mated several times with either the same male or with other males. According to Gilbertson (1925), sunlight apparently acts as a stimulus to bring about mating in species of Chloropidae, at least in *Meromyza americana* Fitch. No male guarding of recently mated females was observed.

During copulation, the male positioned himself above the female with his head directly over the posterior part of her scutellum. He was positioned at about a 40° angle to the larger female, with the terminal end of his abdomen strongly curved downwards to meet the female's genitalia. His wings were folded; the female's wings were spread laterally at about a 45° angle from her body. The male's foretarsi were placed on the wing bases of the female, although they were seen occasionally to grasp her costal vein near the wing bases. His middle tarsi were tightly appressed against the middle of the female's abdomen, about two-thirds of the way back, and his hind tarsi either grasped the copulatory organs of the female or manipulated her genitalia. On several occasions the male extended his proboscis and touched the female's scutellum. During mating both sexes frequently had the wings folded over their abdomens, with the apical portion of the female's wings being bent downward. However, in most cases, the mating position consisted of the female extending her wings laterally away from her body. Adults usually remained in coitus for 45–65 minutes, although one copulation lasted nearly 2.5 hours.

The preoviposition period lasted between 8 to 12 days ($\bar{x}$ = 9, N = 10). Females collected in nature as well as those reared in the laboratory readily oviposited in the breeding jars. In nature, eggs usually were found on the upper surface of the leaves of the host plant close to the culm. They were also found on the stem close to a leaf sheath or between the sheath and the stem. In contrast, females held in breeding jars showed no obvious preference for a particular oviposition site and scattered their eggs over all parts of the host plant as well as on the sides and netting of the container. However, no eggs were found on the moist peat moss substrate. Eggs that had been deposited on leaves of the host plant usually were so oriented that their longitudinal axes were parallel to the veins of the leaf.

During oviposition, the last three abdominal segments were extended to form a telescopic tube. The female used this structure to probe the surface of the host plant for a few seconds before depositing an egg. Each oviposition required only a few seconds, with eggs being attached to the substrate by a glue-like material. In nature, eggs of *E. exilis* were deposited singly, with only 1 or 2 per host plant.

Four laboratory-reared females deposited 40, 48, 50, and 55 eggs, respectively, over a 10 to 12 day period. An average of 5 eggs per female was deposited daily. The incubation period lasted 8–10 days. Shortly before hatching, the mouthhooks of the larvae rubbed against the inner surface of the egg. Typically, larvae required 30–35 minutes to escape the egg membranes.

A newly hatched larva crawled down into or around the ligule of the culm until it reached the slit in the overlapping sheathing portion of the leaves. After entering the space between the leaves, the larva continued to move downwards along the edges of the leaves until it reached the soft succulent tissues at the base of the stem. Minute feeding trails were formed during this initial movement downward. Once at the stem base, the larva penetrated the successive layers by cutting inwards and downwards in a spiral manner until it reached the center of the shoot. Most of the feeding by the second and third instars occurred at the base of the stem, with most

of the tissue near the center of the culm being destroyed. Larvae were found in nature in culms of *C. crinita, C. lacustris,* and *C. lurida* Wahlenb., but not in *C. stricta.*

Larvae apparently rasped the plant tissues with their mandibles, causing cells to rupture and exude sap. The plant juices and the damaged tissues were then ingested. Areas being fed upon quickly became filled with decomposing plant tissue and fecal material that formed conspicuous feeding trails within the stems. Infested plants were easily recognized by the presence of these feeding trails. Plants that were in flower were rarely attacked, possibly because the stem tissues had become tough and fibrous.

The first larval stadium lasted 24–36 hours; the second, 1–2 weeks; and the third, 40–52 weeks. After overwintering, a mature larva reversed direction in the stem and moved upwards between the ensheathing leaves. It then defecated before forming a puparium about 2.5 cm below the ligule of the leaf sheath. The prepupal period lasted 2–3 days; the pupal period, 10–11 days for males (N = 12) and 12–14 days for females (N = 10).

Epichlorops exilis was an univoltine species in northern Ohio. Adults emerged in nature between mid-May and early June. Adult populations remained quite high until mid-June but then declined dramatically (Fig. 43). The earliest collection date for an adult was May 16; the latest, June 30. Overwintering occurred as nearly mature larvae in a state of temperature-induced quiescence, usually below ground level, at the base of the stem of the host plant. Larvae that had overwintered were observed to feed for a few days in early April before migrating upwards in the culm during early May to form puparia.

DESCRIPTIONS OF IMMATURE STAGES

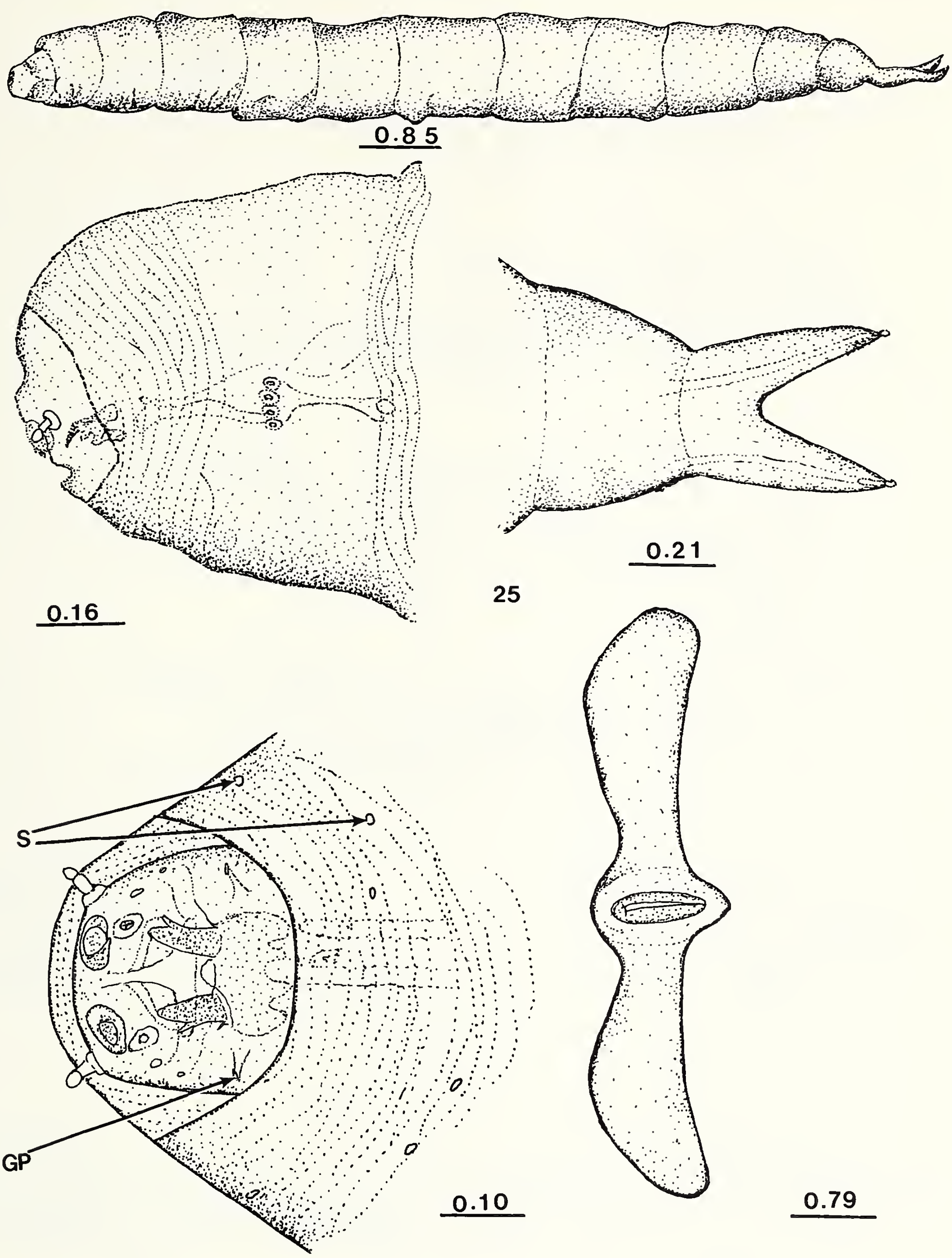
Chlorops certimus

Egg (Fig. 34): Length 0.89–0.93 mm, maximum width 0.18–0.19 mm. Slightly flattened dorsoventrally, tapering anteriorly with micropylar end smaller than rounded posterior end. Ventral surface slightly flattened. Chorion with thin ridges anastomosing and forming delicate reticulations. Areas between ridges with indistinct bead-like pattern.

First instar larva: Similar to third instar except in following characters. Length 0.91–1.64 mm, greatest width 0.15–0.27 mm. Cylindrical to conical. Posterior fleshy projection (Fig. 36) smaller, with 2 short, stout spines distally. Stigmatic chamber and clear areas (Fig. 37) indistinct, only distal spines (reduced spiracular hairs) conspicuous. Thoracic and abdominal segments each with 2 dorsal and 2 lateral spines. Larva metapneustic. Cephalopharyngeal skeleton (Fig. 35) length 0.16–0.18 mm, greatest width 0.02–0.03 mm; lightly pigmented; dorsal and ventral cornua hyaline; hypopharygeal sclerite with 1 clear window.

Second instar larva: Similar to third instar except in following characters. Length 1.69–2.68 mm, greatest width 0.21–0.34 mm. Anterior spiracles (Fig. 41) smaller, inconspicuous, with 3–4 marginal papillae. Cephalopharyngeal skeleton (Fig. 33) length 0.36–0.39 mm, greatest width 0.08–0.09 mm.

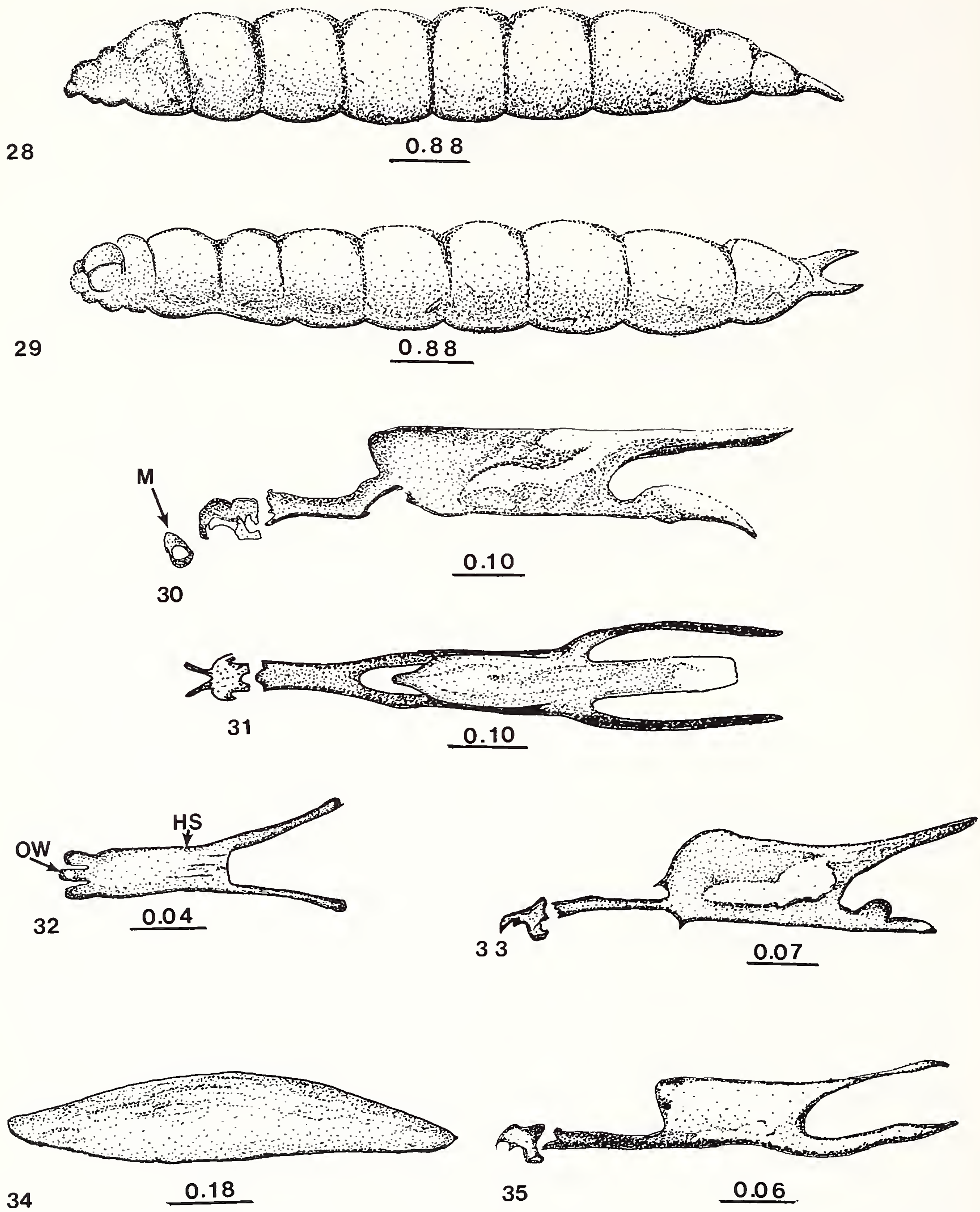
Third instar larva (Fig. 23): Length 6.69–8.13 mm, greatest width 0.79–1.15 mm. Creamy white to opaque, integument transparent to translucent, spinulose and shiny. Body elongate, somewhat flattened dorsoventrally, tapering slightly anteriorly; amphipneustic. Posterior end bilobed and terminating in 2 slightly elongate, barrel-



23 24 25 26 27

Figs. 23–27. *Chlorops certimus,* third instar. 23. Lateral habitus. 24. Lateral view of anterior end. 25. Dorsal view of posterior segment. 26. Ventral view of anterior end showing facial mask. 27. Perianal pad.

shaped spiracular tubes. Segment 1 (cephalic) (Figs. 24, 26) highly retractile, bilobed anteriorly; each lobe bearing short fleshy, 3-segmented antenna, maxillary palp with 6–8 sensory pegs, and genal palp with 1 sensory peg; oral ridges bordering mouth opening not bifurcating. Segment 2 (prothoracic) with 30–35 irregular rows of v-shaped



Figs. 28–35. *Chlorops certimus*. 28. Puparium, lateral habitus. 29. Same, dorsal habitus. 30. Third instar, lateral view of cephalopharyngeal skeleton. 31. Same, dorsal view. 32. Same, dorsal view of hypopharyngeal sclerite. 33. Second instar, lateral view of cephalopharyngeal skeleton. 34. Egg. 35. First instar, lateral view of cephalopharyngeal skeleton.

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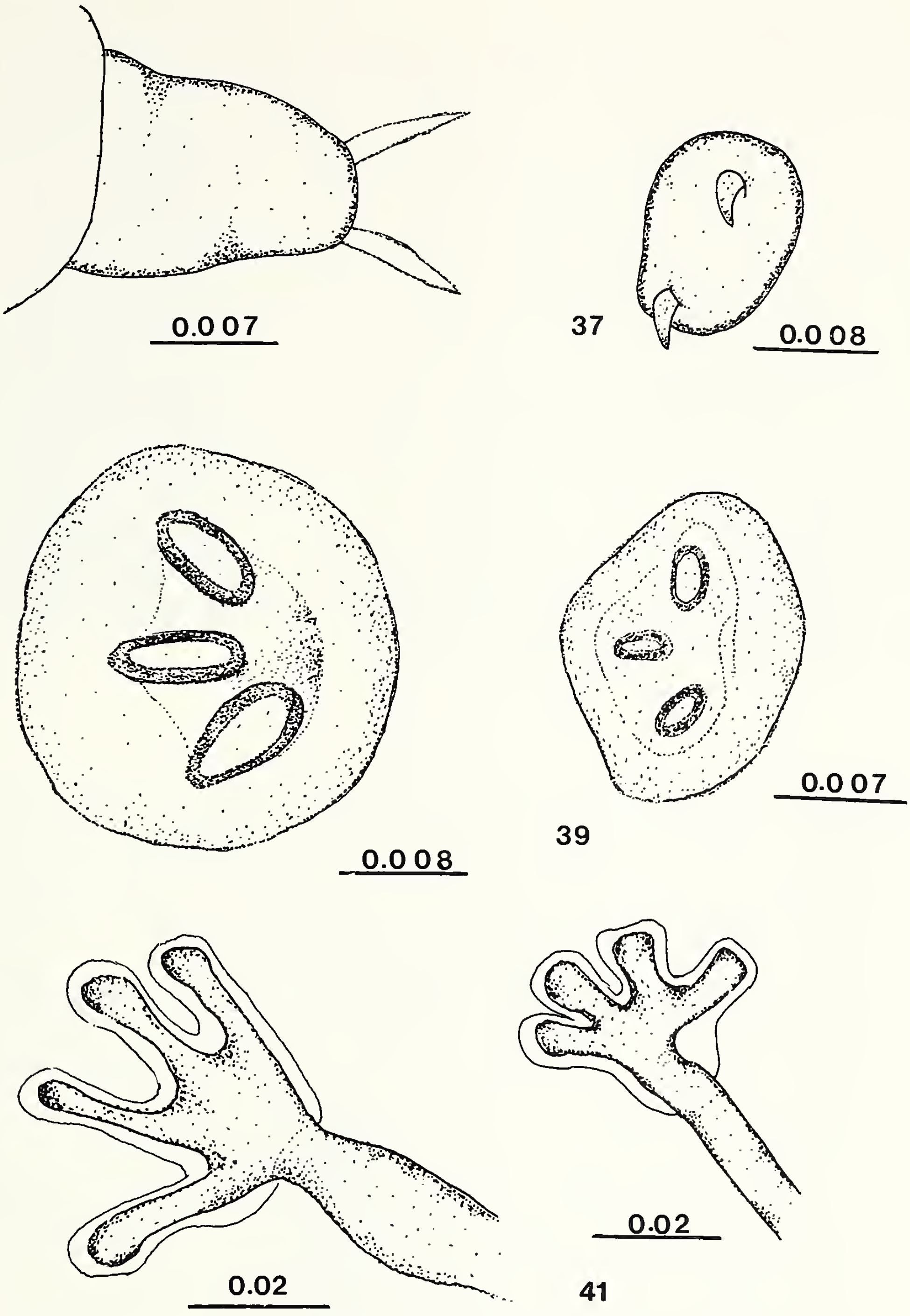


Figs. 36–41. *Chlorops certimus*. 36. First instar, dorsal view of posterior end. 37. Same, posterior spiracular plate. 38. Third instar, same. 39. Second instar, same. 40. Third instar, anterior spiracle. 41. Second instar, same.

spinules encircling segment; with 6 sensory sensilla on ventral surface, each sensillum surrounded by thick triangular spinules. Segments 3–12 with 15–20 small, reduced spinule rows, these becoming indistinct fine lines anteriorly, only 5–10 rows encircling anterior portion of each segment. Primary integumentary folds between abdominal segments with 25–35 or more rows of reduced spinules. Posterior segment (Fig. 25) tapered and terminating in 2 elongate, somewhat triangular fleshy projections. Perianal pad (Fig. 27) bilobed, with anal slit medially, no spinule patch near pad.

Anterior spiracles (Fig. 40) fan-shaped, with 4 apical papillae, each papilla surrounded by transparent membrane.

Posterior spiracles distally at apices of 2 fleshy projections. Spiracular plates indistinct (Fig. 38), with 3 spiracular openings but no spiracular hairs.

Cephalopharyngeal skeleton (Figs. 30, 31) length 0.58–0.61 mm, greatest width 0.11–0.13 mm; heavily pigmented except for light areas on posterior ends of cornua; hypopharyngeal sclerite (Fig. 32) H-shaped, fused with lightly pigmented tentoropharyngeal sclerite; hypopharyngeal plate extending anteroventrally, with anterior oval window and 4 smaller lateral windows; dorsal cornua not connected anterodorsally; floor of tentoropharyngeal sclerite lacking pharnygeal ridges, sclerite lightly pigmented; mandibles fused posterodorsally, deeply pigmented except on accessory teeth and lateral processes; hook part strongly decurved, with sharp accessory tooth.

Puparium (Figs. 28, 29): Elongate with both ends flattened dorsoventrally, segments 1–4 with noticeable lateral ridges. Cuticle thin and transparent, with contained pupa visible; spinule pattern that of mature larva. Length 7.68–7.71 mm, greatest width 1.78–1.80 mm. Anterior spiracles anterolaterad on first apparent segment, with 4 inconspicuous apical papillae. Posterior spiracular tubes elongate, abruptly tapered, and somewhat triangular. Posterior spiracular plates indistinct, and slightly turned upward. Perianal pad as in mature larva.

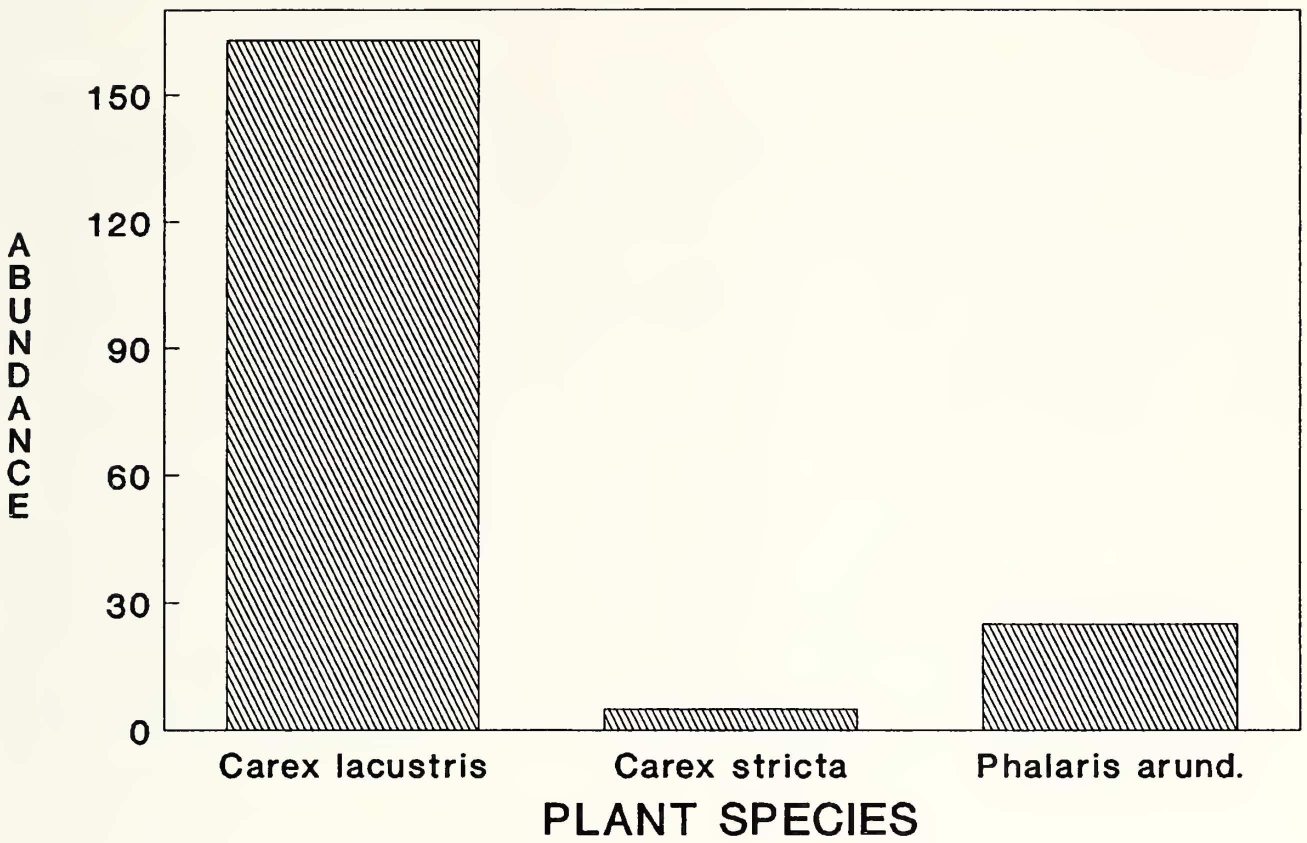
Epichlorops exilis

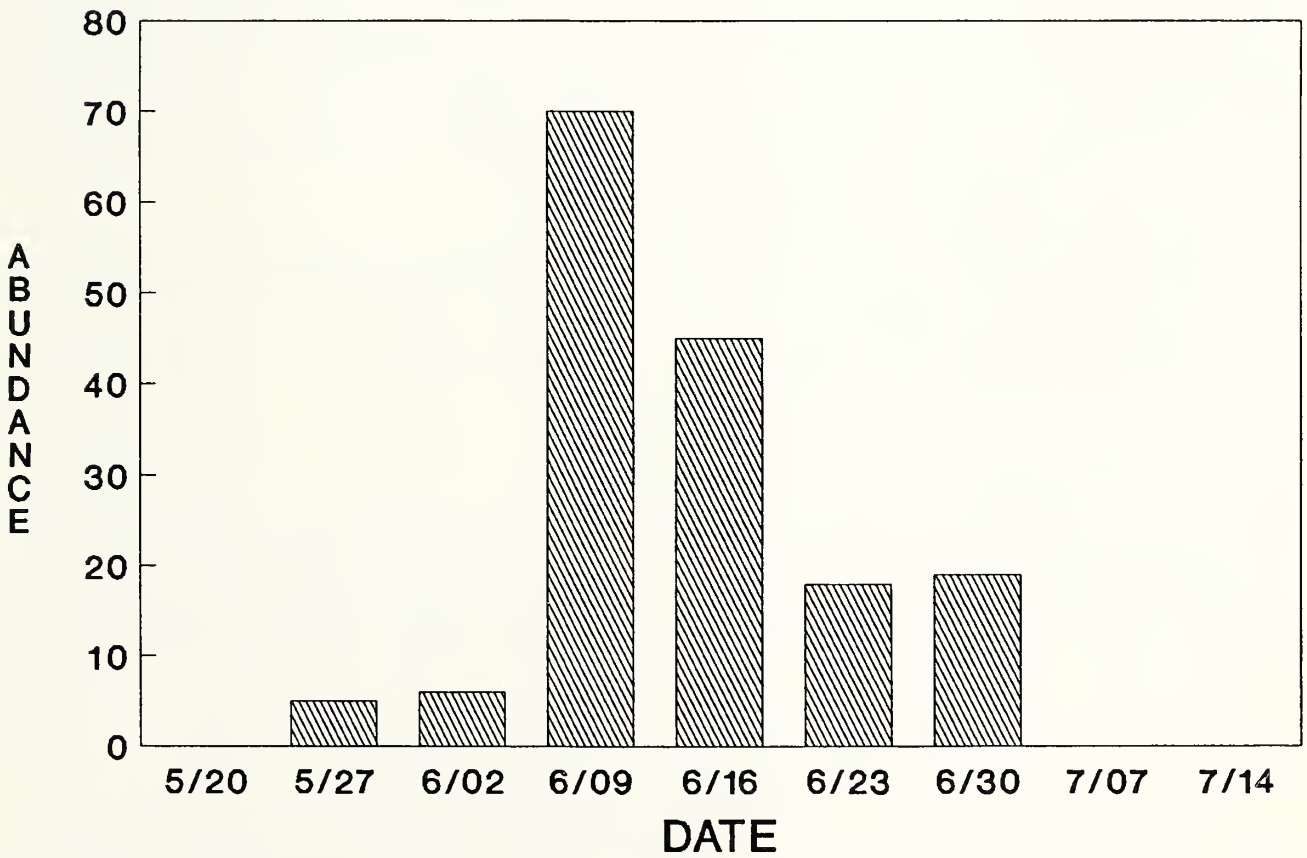
Egg (Fig. 14): Length 1.35–1.70 mm, greatest width 0.19–0.21 mm. White to semitransparent, slightly flattened dorsoventrally. Micropylar end tapering and slightly smaller than rounded posterior end, micropyle facing downward. Ventral surface somewhat flattened, opaque to translucent, not ridged, and lacking fine reticulation. Chorion otherwise with fine polygonal reticulation pattern.

First instar larva: Similar to third instar except in the following characters. Length 1.80–1.95 mm, greatest width 0.12–0.21 mm. Pale white to translucent, integument spinulose. Body conical to cylindrical. Posterior spiracular plates indistinct, at apices of short spiracular tubes; plates (Fig. 16) with 4 elongate, thin, spiracular hairs; spiracular clear areas indistinct. Larva metapneustic. Segments 2–11 each with 2 lateral and 2 dorsal spines (Fig. 17 top, bottom) all projecting posteriorly. Segment 12 with dense dorsoventral spinule patch with 10–15 rows completely encircling segment. Cephalopharyngeal skeleton (Fig. 13) length 0.28–0.30 mm, greatest width 0.04–0.05 mm; tentoropharyngeal sclerite lightly pigmented, fused with hypopharyngeal sclerite; latter sclerite projecting under posteroventral portions of mandibles; mandibles paired, slightly pigmented and fused posterodorsally; hook part, accessory tooth and lateral process lightly pigmented. Accessory tooth arising from side in lateral view.

Second instar larva: Similar to third instar except in the following characters. Length 2.45–2.85 mm, greatest width 0.61–0.71 mm. Pale white to transparent, integument spinulose. Posterior spiracular plate (Fig. 21) smaller, slightly circular to oval, without spiracular hairs. Anterior spiracles (Fig. 19) short and inconspicuous, lightly pigmented, with 5 marginal papillae; each papilla surrounded by transparent membrane. Cephalopharyngeal skeleton (Fig. 12) length 0.47–0.50 mm, greatest width 0.06–0.08 mm. Faintly to moderately pigmented; cornua hyaline; paired mandibles (Fig. 11) fused and heavily pigmented dorsoposteriorly; hook part, accessory tooth, and lateral process lightly pigmented.

Third instar larva (Fig. 1): Similar to that of *C. certimus* except in following characters. Length 7.92–9.37 mm, maximum width 1.52–1.54 mm from thoracic





Figs. 42–43. *Epichlorops exilis.* 42. Distribution of adults in three stands of marsh monocots near Kent, Ohio. 43. Seasonal distribution of adults in stand of *Carex lacustris* near Kent, Ohio.

segment 3; amphipneustic. Segment 1 (Figs. 2, 4) with base of antenna platelike (Fig. 20); maxillary palp consisting of laterally thickened, pigmented ring encircling 5–6 sensory pegs; preoral palp just below maxillary palps consisting of 2 sensory pegs; each lobe also bearing lateral papilla and sharing medioventral, circular to lightly oval sensory plate with 2 sensory papillae; oral ridges not bifurcating, directed towards oral opening. Segment 2 (Fig. 2) bearing anterior spiracles posterolaterally. Perianal pad (Fig. 5) as in *C. certimus.* Anterior spiracles (Fig. 18) conspicuous, fan-shaped, bearing 5–6 apical papillae. Each papilla slightly pigmented, and surrounded by transparent membrane. Posterior spiracles (Fig. 3) similar to those of *C. certimus.*

Cephalopharyngeal skeleton (Figs. 8, 9) length 0.74–0.80 mm, greatest width 0.13–0.16 mm; hypopharyngeal sclerite (Fig. 10) with hypopharyngeal plate with clear oval window, middle of plate heavily pigmented with 2 small clear windows and two lateral notches; mandibles (Fig. 15) very similar to those of *C. certimus.*

Puparium: Very similar to that of *C. certimus* except in following characters. Length 9.00–9.16 mm, greatest width 0.89–0.92 mm. Anterior spiracles with 5–6 apical papillae. Posterior spiracular plates deeply pigmented, rounded, and slightly turned upward; spiracular openings distinct.

DISCUSSION

Although the larval feeding habits of only 15–20% of the Nearctic Chloropidae are known, several species have been found to have saprophagous larvae (Valley et al., 1969). This suggests that the ancestral Chloropidae were also scavengers. This is in agreement with Oldroyd (1964), who speculated that all modern groups of Diptera evolved from compost-feeding ancestors. If so, the precursors of such present-day primary invaders as the species of *Chlorops* and *Epichlorops* may be best typified by the rather generalized way of life found in the genus *Elachiptera.* Larvae of this genus develop equally well on leaf mold, rotting vegetation, and decaying wood (Oldroyd, 1964). Possibly, the evolutionary pathway leading to phytophagy was from scavenging on decaying plant material to being a secondary invader of plant tissues damaged by some primary invader to being truly phytophagious.

Seemingly unique (apomorphic?) for the phytophagous Chloropinae are the fleshy lobes (stigmatophores) that project posteriorly from the caudal segment (Fig. 3). Nowicki (1873) was the first to note these lobes and suggested that they were taxonomically significant. Similar lobes have not been found in any of the secondary invaders that have been investigated. Wearsch (1968) described them in larvae of *Diplotoxa,* which feed as primary invaders in stems and rhizomes of spike-rush (*Eleocharis* spp.). Mature larvae of *Diplotoxa* are easily distinguished from those of *Epichlorops* and *Chlorops* in that they all possess 3–4 branching spiracular hairs, whereas larvae of *Epichlorops* and *Chlorops* lack such hairs. The fleshy lobes vary in size, shape, and pigmentation and could prove useful in differentiating closely related species.

The cephalopharyngeal skeletons of *C. certimus* and *E. exilis* larvae are very similar (Figs. 8, 30). Mandibles of the third instar larva (Fig. 15) typically consist of a large, heavily sclerotized apical hookpart, a lightly pigmented accessory tooth, and a moderately pigmented lateral process. The mandibles rasp and cut through the plant tissues, enabling larvae to feed on the exuding cellular protoplasm. Perhaps the most interesting speculation about the cephalopharnygeal skeleton concerns the lateral

processes that project from the posterolateral portions of the mandibles (Fig. 15). These slightly upward-curving projections appear to be characteristic of *Chlorops* and *Epichlorops.* Judging from the illustrations of Valley (1968), the lateral processes may have evolved from the fusion of the dental sclerites with the mandibles. Originally, the dental sclerites probably were very similar to those found today in *Lasiosina canadensis* Aldrich (Valley, 1968). The position of the dental sclerites and their degree of fusion with the mandibles appear to reflect the feeding habits of the larvae. In *L. canadensis,* a secondary invader, the dental sclerites are closely associated with the mandibles but not fused to them. Possibly they provide areas for muscle attachment that help coordinate movements of the mandible. In *Meromyza americana,* a primary invader of grasses, the dental sclerites (as illustrated by Allen and Painter, 1937) are larger, slightly arched, and partially fused to the mandibles. In *Epichlorops* and *Chlorops,* which have somewhat similar feeding habits, there are no obvious dental sclerites. However, the lateral processes are well developed and very similar morphologically to the partially fused dental sclerites shown in *M. americana.* This suggests that in *Chlorops* and *Epichlorops* the dental sclerites have become solidly fused to the mandibles.

The shape of the tentoropharyngeal sclerite of *Epichlorops* and *Chlorops* also appears to reflect the larval feeding habits. Unlike those of such secondary invaders as *L. canadensis* and *Elachiptera costata* (Loew), larvae of the primary invaders lack longitudinal ridges in the floor of the pharnyx. Pharyngeal ridges have been reported in scavenging larvae of Otitidae, Lauxiniidae, Ephydridae, and several other families of muscomorphous Diptera. Presence or absence of the pharnygeal ridges may reflect the nutritional value of the liquid portions of the food substrate. According to Dowding (1987), pharnygeal ridges function as a sieve that filters out and concentrates small food particles from a semiliquid substrate. The ridges, therefore, are advantageous to scavenging larvae that are essentially particle feeders. However, larvae of *Epichlorops* and *Chlorops* utilize highly nutritious protoplasm, and there would be no selective advantage in retaining pharyngeal ridges.

The mature larvae of *C. certimus* and *E. exilis* are very similar, and the two species cannot be readily distinguished. The anterior spiracles of *C. certimus* possess only 4 marginal papillae, whereas those of *E. exilis* have 5–6 papillae. In contrast, the first instars of *E. exilis* are easily distinguished from those of *C. certimus* by the presence of four elongate, non-branching spiracular hairs in the former species (Fig. 16).

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EXPLANATION OF LABELS ON FIGURES

A, antenna; ASl, anal slit; ASp, anterior spiracle (m, membrane); AT, accessory tooth; Cph, cephalopharyngeal skeleton; DC, dorsal cornu; DS, dorsal spine; GP, genal papilla; HS, hypopharyngeal sclerite; LP, lateral process; LS, lateral spine; M, mandible (bp, basal part, hp,

hook part); MP, maxillary palp; OW, oval window; Pa, papilla; PO, preoral palp; PP, perianal pad; PSp, posterior spiracle; S, sensilla; StC, stigmatic chamber; SO, spiracular opening; TS, tentoropharyngeal sclerite; VC, ventral cornu.

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RELATIONSHIPS BETWEEN SIZES OF MORPHOLOGICAL FEATURES IN WORKER HONEY BEES (*APIS MELLIFERA*)

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Abstract.—Three important morphological attributes of 100 worker honey bees (*Apis mellifera* L.) from each of four colonies were examined morphometrically. Intertegular span (a measure of overall size), corbicular area (a measure of pollen carrying potential), and wing measurement C (highly correlated to functional proboscis length) were the morphological features selected. Worker bees with larger intertegular spans (or corbiculae, or wing measurements C) did not possess other morphological features that were highly correlated in size. This lack of correspondence was true in analyses focusing upon both linear and allometric size relationships. The lack of strong size correlations between morphological features is discussed in terms of both artificial and natural selection acting upon honey bee colonies.

The worker honey bees (*Apis mellifera* L.) present in a colony occur in a range of sizes which, although modest compared to the intracolonial worker size range of bumblebees (Plowright and Laverty, 1984), is nonetheless a significant factor in worker task performance. Among honey bees heavier foragers collect larger nectar loads, with an average ratio between load weight and unladen body weight of 82% (Wells and Giacchino, 1968). Measurements within a colony of the number of dance circuits per time indicate that larger bodied pollen foragers fly further than smaller bees (Waddington, 1988). Foragers collected from artificial feeders located at greater distances from a hive are larger than those collected at closer feeders (Waddington, 1988). Workers with larger corbiculae carry larger pollen loads back to their colony and gather more honey (Milne and Pries, 1986, 1984). Larger foragers go on more frequent foraging trips, although trip duration does not vary with body size (Cideciyan, 1984). Worker size variability among honey bees may also influence the effectiveness of dance communication (Waddington, 1989, 1988, 1981).

Larger worker honey bees might possess uniformly larger morphological features. In this case a worker with larger flight muscles would also have larger corbiculae (and hence the potential to collect heavier pollen loads) and a longer proboscis (which might improve foraging speed and breadth, as it is known to do in bumble bees (Waddington and Herbst, 1987; Plowright and Laverty, 1984; Harder, 1982; Inouye, 1980; Corbet, 1978)). However, there is reason to believe that this correspondence in sizes of morphological features might not be true in honey bees. Honey bees bred for high colonial pollen hoarding characteristics acquire larger corbiculae without larger overall body sizes (Milne et al., 1986). If artificial selection can increase the size of one morphological feature of honey bees independently of other features, is there typically any correlation between the sizes of important morphological attributes of worker bees?

In this study we selected three important morphological features of worker honey

bees, and measured the sizes of these features on 100 bees from each of four colonies. Analyses using regression techniques to examine the possibilities of either linear correlations or allometric relationships among these features (Oster and Wilson, 1978) were carried out.

MATERIALS AND METHODS

Four colonies of Carniolan honey bees bred from New World stocks were established in early spring using artificially inseminated sister queens. Each queen received 2 microliters of mixed semen. The semen used to inseminate each queen was taken from seven drones, each of which was produced by one of seven mother queens. The four colonies therefore each contained 7 patrilines, with the greatest amount of genetic similarity possible between colonies. This was intended to reduce differences between colonies based upon patrilineal variability (reviewed in Kolmes et al., 1989).

In August, workers for morphometric analysis were shaken from the end frames of each colony into separate jars of ethanol. One hundred bees per colony were analyzed morphometrically using a Wild M5 dissecting microscope equipped with ocular micrometers. Corbicular areas were measured by multiplying their length times half of their width, using the method devised by Milne and Pries (1984). The wing measurement C of Waddington and Herbst (1987) was used as a highly correlated estimator of functional proboscis length. Intertegular span was used to measure worker size, as Cane (1987) has shown it to be a measurement free of certain complications involved in measuring dry weights (e.g., crop contents, glandular secretion storage, pollen loads). All of the 400 workers were measured for all three of the preceding morphological characteristics.

Data were analyzed using linear regression techniques. In order to determine whether corbicular areas, wing measurements C, and intertegular spans all increased or decreased in size together, pairwise linear regressions for these characteristics for the 100 workers from each hive were calculated. In order to examine the possibility of nonlinear but allometric relationships between the sizes of these morphological features, base 10 logarithms of all 1,200 morphometric values were computed and pairwise linear regression analyses for these logarithmic values for the 100 workers from each hive were calculated. This corresponds to the definition of allometric relationships given in Oster and Wilson (1978), as ". . . the sizes of two parts will be related by a simple power law: $\log y = \log b + a \log x$, or, equivalently, $y = bx^a$ where y and x are linear measures of the two body parts and a and b are fitted constants the values of which depend on the nature of the measurement taken. (p. 129)"

The significances of the regression analyses were evaluated with reference to the two possible endpoints for correlations between different morphological characteristics. On one hand, there might be absolutely no relationship between the sizes of different body parts of worker bees, which is equivalent to a first null hypothesis that the sample of data was drawn from a population with a parametric correlation coefficient of zero. This was tested by comparing r^2 values to tabular critical values. This procedure is preferable to evaluating the significances of the slopes of the regression lines in situations where the goal is to establish an association between variables (Keppel and Saufley, 1980).

The second possible endpoint is the case of highly correlated morphological fea-

Table 1. Mean and SE mean values for intertegular spans (mm), wing measurements C (mm), and corbicular areas (mm^2) for 100 workers each from colonies 84, 85, 86, and 88.

	Mean	SE mean
Colony 84		
Intertegular span	2.93	0.017
Wing-C	3.96	0.010
Corbicular area	1.36	0.012
Colony 85		
Intertegular span	2.99	0.016
Wing-C	4.08	0.009
Corbicular area	1.42	0.010
Colony 86		
Intertegular span	3.07	0.018
Wing-C	4.06	0.012
Corbicular area	1.39	0.010
Colony 88		
Intertegular span	2.97	0.017
Wing-C	4.02	0.009
Corbicular area	1.44	0.010

tures, and here we can turn to the literature for r^2 values that will make an appropriate comparison. Examples of known *Apis mellifera* morphometric features with values that are highly correlated with one another include the relationship between wing measurement C and proboscis length ($r^2 = 50\%$), and the even more highly correlated relationships between head width and wing measurement C ($r^2 = 86\%$) or between wing measurement A and wing measurement C ($r^2 = 94\%$) reported by Waddington and Herbst (1987). Examples from other bee species include the intertegular span and dry weight linear relationship ($r^2 = 95\%$) for *Diadasia rinconis* (Cane, 1987), and the correlations between wing length and proboscis length approximating 90% for four species of *Bombus* (Morse, 1977). We might expect the correlations between morphological features to be lower in honey bees than in bumble bees because of the lower variation in body size among workers of *A. mellifera* (Waddington and Herbst, 1987), but an r^2 value much lower than 50% is below that which we can reasonably expect for strongly correlated morphological features even among workers of a species with a modest range of sizes. When an r^2 value is much lower than these comparison r^2 values, we can reject the second null hypothesis that the morphometric variables are strongly correlated to one another. The value of $1 - r^2$ (the coefficient of nondetermination) expresses the proportion of the variation in one morphological feature that is not accounted for, or not held in common between the two variables (Keppel and Saufley, 1980).

RESULTS

The mean values and standard errors of the mean values for intertegular spans, wing measurements C, and corbicular areas were similar for the workers from the

Table 2. Regression analysis of morphological measures done in a pairwise fashion.

	r^2	Regression equation
Colony 84		
Intertegular span vs. wing measurement C	2.4%	int. = 1.84 + 0.28 wing
Intertegular span vs. corbicular area	5.9%	int. = 2.43 + 0.36 corb.
Wing measurement C vs. corbicular area	5.2%	wing = 3.70 + 0.19 corb.
Colony 85		
Intertegular span vs. wing measurement C	0.0%	int. = 3.11 − 0.03 wing
Intertegular span vs. corbicular area	0.8%	int. = 2.77 − 0.16 corb.
Wing measurement C vs. corbicular area	0.0%	wing = 4.07 + 0.01 corb.
Colony 86		
Intertegular span vs. wing measurement C	9.4%	int. = 1.11 + 0.48 wing
Intertegular span vs. corbicular area	3.3%	int. = 2.63 + 0.32 corb.
Wing measurement C vs. corbicular area	0.9%	wing = 3.92 + 0.11 corb.
Colony 88		
Intertegular span vs. wing measurement C	0.0%	int. = 2.97 + 0.002 wing
Intertegular span vs. corbicular area	2.5%	int. = 2.58 + 0.27 corb.
Wing measurement C vs. corbicular area	0.3%	wing = 4.10 − 0.05 corb.

four colonies (Table 1). The standard errors of the mean values were a small percentage of the mean values.

For none of the morphological characteristics measured was there ever a close correlation when their r^2 values were evaluated with reference to r^2 values for tightly correlated morphometric features (Table 2). The r^2 values (expressing the strength of the correlation between the two variables being examined) ranged from 0.0% to 9.4%, with an average $r^2 = 2.6\%$. Even the highest r^2 value indicated that the proportion of variation in one morphometric feature not accounted for (or held in common) between the two variables exceeded 90%. Therefore intertegular spans, wing measurements C, and corbicular areas did not increase or decrease together in a linear fashion among worker honey bees.

When regression analysis was carried out upon the logarithms of the morphological measurements to look for allometric relationships between body parts, the results were similar to those obtained using the untransformed data. Table 3 reports the r^2 values for linear regressions carried out on log transformed data. The r^2 values range from 0.0% to 9.7%, with an average $r^2 = 2.6\%$. Even the highest r^2 indicated that the proportion of variation in one morphometric feature not accounted for (or held in common) between the two variables exceeded 90%. No reasonably strong allometric relationship between the morphological measures was apparent.

For none of the three pairs of morphometric measures (Table 2) was the r^2 value averaged over all 4 colonies significantly different from that expected for a population with parametric correlation coefficients equal to zero (all $P > 0.05$). Of the 12 individual r^2 values for the data expressed in linear form (Table 2) evaluated for a significant deviation from $r^2 = 0$, in only one instance (colony 86, intertegular span vs. wing measurement C) was the difference from $r^2 = 0$ significant at $P < 0.01$ (df

Table 3. Regression analysis of logarithms of morphological measures done in a pairwise fashion.

	r^2	Regression equation
Colony 84		
Log (intertegular span) vs. log (wing measurement C)	2.5%	$\log(i) = 0.24 + 0.38 \log(w)$
Log (intertegular span) vs. log (corbicular area)	5.2%	$\log(i) = 0.45 + 0.13 \log(c)$
Log (wing measurement C) vs. log (corbicular area)	5.1%	$\log(w) = 0.59 + 0.05 \log(c)$
Colony 85		
Log (intertegular span) vs. log (wing measurement C)	0.0%	$\log(i) = 0.50 - 0.04 \log(w)$
Log (intertegular span) vs. log (corbicular area)	0.7%	$\log(i) = 0.47 + 0.07 \log(c)$
Log (wing measurement C) vs. log (corbicular area)	0.0%	$\log(w) = 0.61 - 0.0003 \log(c)$
Colony 86		
Log (intertegular span) vs. log (wing measurement C)	9.7%	$\log(i) = 0.09 + 0.65 \log(w)$
Log (intertegular span) vs. log (corbicular area)	3.9%	$\log(i) = 0.46 + 0.16 \log(c)$
Log (wing measurement C) vs. log (corbicular area)	1.1%	$\log(w) = 0.60 + 0.04 \log(c)$
Colony 88		
Log (intertegular span) vs. log (wing measurement C)	0.0%	$\log(i) = 0.47 + 0.01 \log(w)$
Log (intertegular span) vs. log (corbicular area)	2.5%	$\log(i) = 0.45 + 0.13 \log(c)$
Log (wing measurement C) vs. log (corbicular area)	0.3%	$\log(w) = 0.61 - 0.02 \log(c)$

= 98, $r^2_{0.01} = 6.7\%$). In two other instances (colony 84, intertegular span vs. corbicular area; colony 84, wing measurement C vs. corbicular area) there were differences from $r^2 = 0$ that were significant at $P < 0.05$ (df = 98, $r^2_{0.05} = 4.0\%$), but an alpha level of 0.05 is not far from the level likely to generate spuriously significant results when this many identical statistical tests are being carried out. None of the other nine individual r^2 values differed significantly from 0 (all $P > 0.05$).

For none of the three pairs of logarithms of morphometric measures (Table 3) was the r^2 value averaged over all 4 colonies significantly different from that expected for a population with parametric correlation coefficients equal to zero (all $P > 0.05$). Of the 12 individual r^2 values for the data expressed in logarithmic form (Table 3) evaluated for a significant deviation from $r^2 = 0$, in only one instance (colony 86, log(intertegular span) vs. log(wing measurement C)) was the difference from $r^2 = 0$ significant at $P < 0.01$ (df = 98, $r^2_{0.01} = 6.7\%$). In two other instances (colony 84,

log(intertegular span) vs. log(corbicular area); colony 84, log(wing measurement C) vs. log(corbicular area)) there were differences from $r^2 = 0$ that were significant at $P < 0.05$ (df = 98, $r^2_{0.05} = 4.0\%$), but again an alpha level of 0.05 is not far from the level likely to generate spuriously significant results when this many identical statistical tests are being carried out. None of the other nine individual r^2 values differed significantly from 0 (all $P > 0.05$).

DISCUSSION

Worker honey bees with larger intertegular spans (or corbiculae, or wing measurements C) did not possess other morphological features that were highly correlated in size. This was true in terms of lacking both linear relationships between morphological attributes (Table 2) and allometric relationships between morphological attributes (Table 3). Larger worker bees are not simply uniformly scaled-up versions of smaller worker bees.

The ability of Milne et al. (1986) to select for larger corbiculae was presumably based upon this loose relationship between the sizes of various morphological features. It is probable that evolutionary flexibility is increased in a system where larger corbiculae or longer proboscises could be selected for independently by environmental circumstances. Such a system would produce a single highly adaptable worker caste, rather than the multiple physical castes based upon allometric growth that are found in the ants and termites (Oster and Wilson, 1978).

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A NEW SPECIES OF *DRYMUSA* (ARANEAE: SCYTODOIDEA) FROM ARGENTINA

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Abstract.—Drymusa serrana, a new species from Buenos Aires Province (Argentina), is described and figured. It represents the first species of *Drymusa* described for South America.

The genus *Drymusa* includes eight described species, three from Africa and five from Central America and the West Indies, and it is included in the superfamily Scytodoidea based on the characters that traditionally defined this group: anterior median eyes absent, indirect eyes forming diads, chelicerae fused in the base with a carinated promargin, and elongated, triangular, convergent maxillary lobes. A ninth species from Argentina is here described for first time; it represents the first species of the genus described for South America.

Some authors (Gertsch, 1967; Valerio, 1971, 1974) include *Drymusa* in the family Scytodidae (*Scytodes, Loxosceles* and *Drymusa*). Alayón (1981, 1987) joins *Loxosceles* and *Drymusa* in a family Loxoscelidae that excludes *Scytodes.* Alternatively, Lehtinen (1986) includes *Drymusa* in its own family, Drymusidae.

The interrelationships of the Scytodoidea are presently very poorly known. Most previous workers have concentrated primarily on the question of ranking the constituent groups, rather than focusing on their composition. Of course, elevating each genus to the rank of family while ignoring their relationships would not resolve anything. Lehtinen (1986) and Alayón (1981) have recently evaluated this issue, but their conclusions are not convincing. Lehtinen's cladogram shows veiy clearly his idea of the interrelationships of the Scytodoidea, but it does not show with the same clarity the characters that support such a hypothesis (it only says "genitalic characters," "claw characters," etc.). Alayón (1981) is more explicit about the characters; he suggests that greater affinities exist between the genera *Drymusa* and *Loxosceles* than between these and *Scytodes.* However, his conclusion is based on the fact that *Drymusa* and *Loxosceles* share the absence of the diagnostic characters of *Scytodes* (female palpal tarsus with two or three modified unguiform setae, very convex cephalothorax, and sclerotized areas behind genital opening in the female). Therefore, Alayón (1987) does not show in his discussion that *Loxosceles* and *Drymusa* are more closely related among themselves, but only that they should not be included within *Scytodes.*

So far, the genus *Drymusa* has not been characterized by any apomorphy. Valerio (1971) says in his diagnosis of the genus that the genital lips are very sclerotized in both sexes (in other related spiders the male genital lips are not sclerotized). If present in all the species previously described, that sclerotization would indicate that they

form a monophyletic group excluding *D. serrana*; however, only females are known for some species. No apomorphies are known for *D. serrana* and the other *Drymusa*. Therefore, until new evidence bearing on this is found, the hypothesis of monophyly of *Drymusa* (either excluding or including *D. serrana*) cannot be defended or rejected on any basis.

Measurements are given in millimeters; all the specimens are deposited in the collection of the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires (MACN).

Drymusa serrana, new species
(Figs. 1–7)

Type. Holotype male, MACN 8752, from Sierra de La Ventana, Buenos Aires Prov., Argentina, P. Goloboff, A. Zanetic Col., Oct. 1980.

Etymology. The specific name refers to the habitat where the specimens were collected.

Diagnosis. It is distinguished from *D. simoni* Bryant and *D. dinora* Valerio by the genital opening located in the anterior part of the abdomen and the much longer male embolus. It is also distinguished from *D. simoni* by the absence of recurved hairs in tibiae and metatarsi I and the lack of a sclerotized lobe in front of the tracheal spiracle, and from *D. dinora* also by lacking the dorsal wrinkles in the abdominal apex. From *D. armasi* Alayón it is distinguished by its color and the greater number of tarsal claw teeth, and from *D. spectata* Alayón by lacking the dense tuft of hairs in the male palpal tarsus and thoracic fovea.

Description (male holotype). Total length, 8.06. Cephalothorax (Fig. 1), 2.80 long, 2.33 wide, low and flattened, without fovea. Anterior median eyes absent, the other six forming diads. Chelicerae with 2 teeth and carina in promargin, a small tooth in retromargin, fused in their base (Figs. 2, 3); fang short, stout and curved. Maxillary lobes elongated, converging in front of the labium, with membranous apical edge. Labium 0.83 long, 0.67 wide, separated from sternum by a suture. Sternum 1.50 long, 1.40 wide, rounded posteriorly.

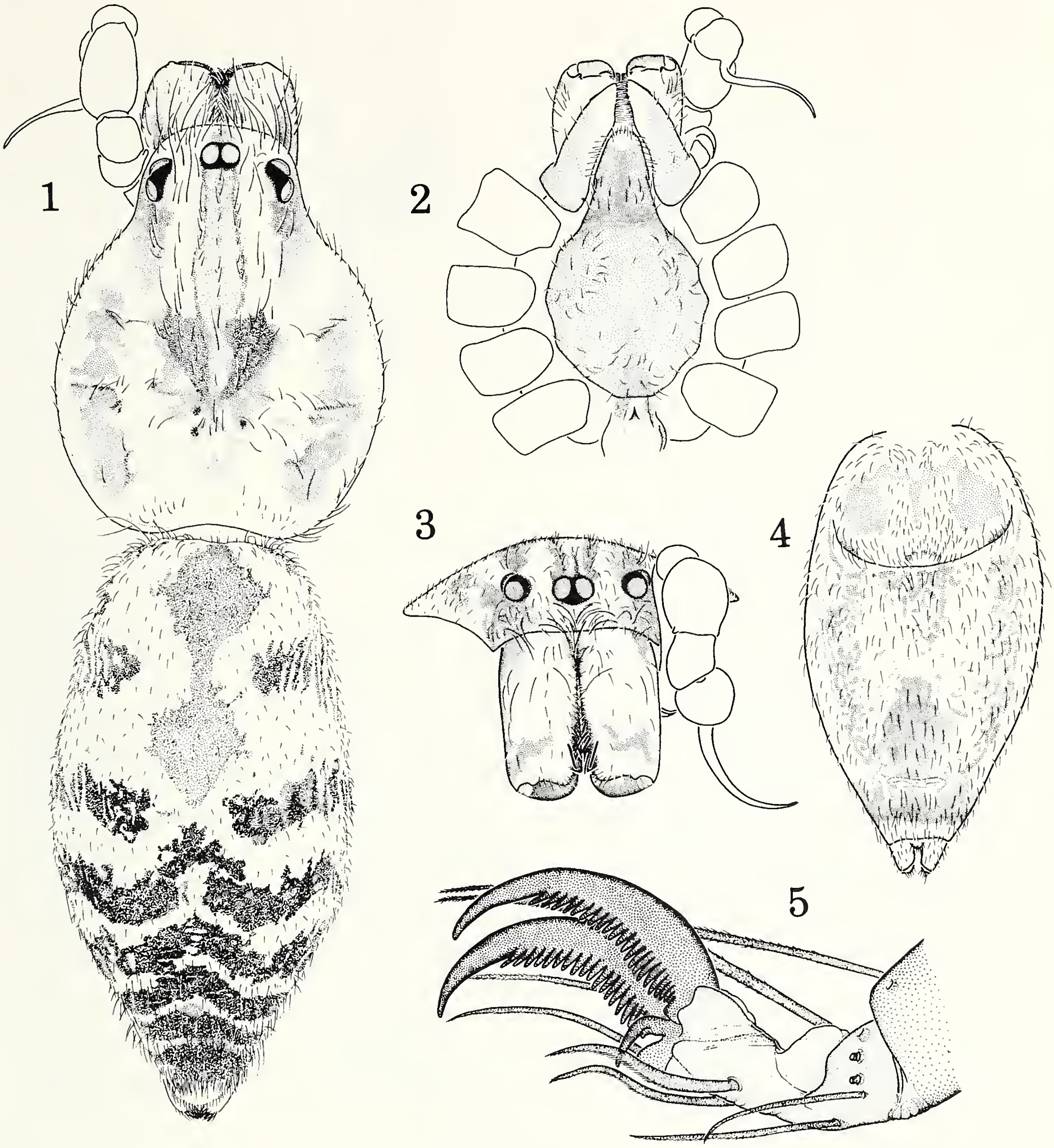
Leg measurements:

	Femur	Patella	Tibia	Metatarsus	Tarsus	Total
I	9.51	0.93	10.77	10.77	1.76	33.74
II	9.04	0.97	8.91	9.18	1.63	29.73
III	6.92	0.90	6.78	6.91	1.50	23.01
IV	8.65	1.00	8.51	8.31	1.96	28.43
Palp	1.00	0.30	0.83	—	0.43	2.56

Tibiae and metatarsi without recurved setae, with filiform and spiniform setae. Tarsi long and thin, ventral face with abundant setae, with spurious claws (serrated bristles) beneath third claw (Fig. 5), with very developed onychium. Paired claws of tarsi I with 15 teeth, of tarsi IV with 22.

Palp: Bulb (Figs. 6, 7) inserted in the cymbial apex, with very long embolus; tarsus with few very long setae; tibia globose.

Abdomen elongated, depressed, posteriorly acute; without wrinkles. Genital open-



FIGS. 1–5. *D. serrana*, new species, male holotype. 1. Dorsal view. 2. Cephalothorax, ventral. 3. Cephalothorax, anterior view. 4. Abdomen, ventral. 5. Claws from tarsus IV.

ing in the anterior third of the abdomen, with little sclerotized lips. Without lobe or sclerotized plate in front of tracheal spiracle. Colulus small but well evident (Fig. 4).

Color: Cephalothorax yellowish, with darker spots; abdomen yellowish, with reddish chevron (Fig. 1).

Female. Unknown.

Natural history. The specimens were collected near the Cerro La Ventana, under big rocks in stream creeks, where the soil is wetter than in the more exposed foothills.

FIGS. 6, 7. *D. serrana,* new species, male holotype, right palp. 6. Retrolateral. 7. Prolateral.

In this type of habitat *Mecicobothrium thorelli* Holmberg, 1881 (Mecicobothriidae) and *Oligoxistre argentinensis* (Mello-Leitão, 1941) (Theraphosidae) are also common.

The spiders were in the inferior face of the rocks; no conspicuous web was observed.

Biogeography. Alayón (1981) offers an explanation of the distribution of *Drymusa* in which he invokes multiple dispersals and predicts that the genus should also be found in South America. *D. serrana* seems to fulfill such expectations and confirm his ideas. However, the presence of the genus in South America is implied by its Gondwanian origin (the vicariant aspect of Alayón's hypothesis) and it is completely unrelated to the dispersals in Central America. The discovery of *D. serrana,* therefore, in no way supports the idea of those dispersals. Hopefully, future studies will show whether the genus fits a general biogeographic pattern; until then, postulating unique causes (such as dispersals) to explain its distribution seems unnecessary.

Other material examined. Same data as the holotype, 4 juveniles (MACN 8754). A juvenile (MACN 8789) from San Luis Prov. (Villa Elena, near Cortaderas, Nov. 10–11, 1982, E. Maury col.) may belong to this species and indicate a wider range.

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Note added in proof: While this paper was in press, Platnick et al. (Am. Mus. Novitates, No. 3016, 73 pp.) analyzed the interrelationships of the Scytodoidea (and other Haplogynae). They conclude that *Drymusa* is more closely related to *Scytodes* than to *Loxosceles.*

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NOTES AND COMMENTS

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NEW DISTRIBUTIONAL RECORDS FOR THE ANT GENUS *PONERA* (HYMENOPTERA: FORMICIDAE) IN NORTH AMERICA

The genus *Ponera* consists of 30 living species, mostly confined to the Indo-Australian area (Taylor, 1967; Terayama, 1986). There are two species found in the New World: *P. pennsylvanica* Buckley and *P. exotica* M. Smith. Both are small, rarely collected ants found in soil and leaf litter, most commonly in mesic areas of the southeastern part of the United States. Little is known about them due to the small colony size and their cryptic habits. *Ponera exotica* has been reported from only a few localities in North Carolina, Florida and Oklahoma (Taylor, 1967; Johnson, 1987). It has close affinities with the Indo-Australian fauna, which led Smith (1962) and Taylor (1967) to conclude that it had been introduced into the New World from that area.

We have studied several series of both species and report on considerable range extensions from Kansas, Arkansas, Louisiana (new state records for *P. exotica*), Texas (new state records for both species) and Michoacan (Mexico, new country record for *P. pennsylvanica*). It is apparent that *P. exotica* is part of our native fauna (Johnson, 1987).

The ants were collected by sieving mesic forest leaf litter from each of the localities through a 1.25 cm mesh sieve, and then extracting the insects using Berlese funnels. Specimens were preserved in 70% ethanol.

Ponera pennsylvanica is widely distributed over much of the eastern and central United States and extreme southern Canada (Fig. 1) and is now reported from southwestern Mexico. New distributional records in the USA include ARKANSAS: Cross Co., Village Creek State Park. Pike Co., Center of Diamonds State Park. Pulaski Co., Pinnacle Mountain State Park. KANSAS: Wallace Co., Sharon Springs. MISSISSIPPI: Clark Co., Clark State Park. TEXAS: Houston Co., Big Slough Wilderness. Polk Co., Big Thicket Natural Preserve. Sabine Co., 3 km W Brookeland and 14.5 km E Hemphill. Smith Co., Tyler State Park. Taylor Co., Big Thicket Natural Preserve and Spurger. Walker Co., Huntsville State Park. Wood Co., 3.5 mi W Hawkins. A

→

Figs. 1, 2. 1. The distribution of *Ponera pennsylvanica*. Circles are our records, stippled areas and squares are from the literature (Taylor, 1967; Browne and Gregg, 1969; DuBois, 1985; Wheeler and Wheeler, 1988). Only collection points at the edge of the range of the distribution are shown. 2. The distribution of *Ponera exotica*. Circles are our records, squares are from literature records (Taylor, 1967; Johnson, 1987).

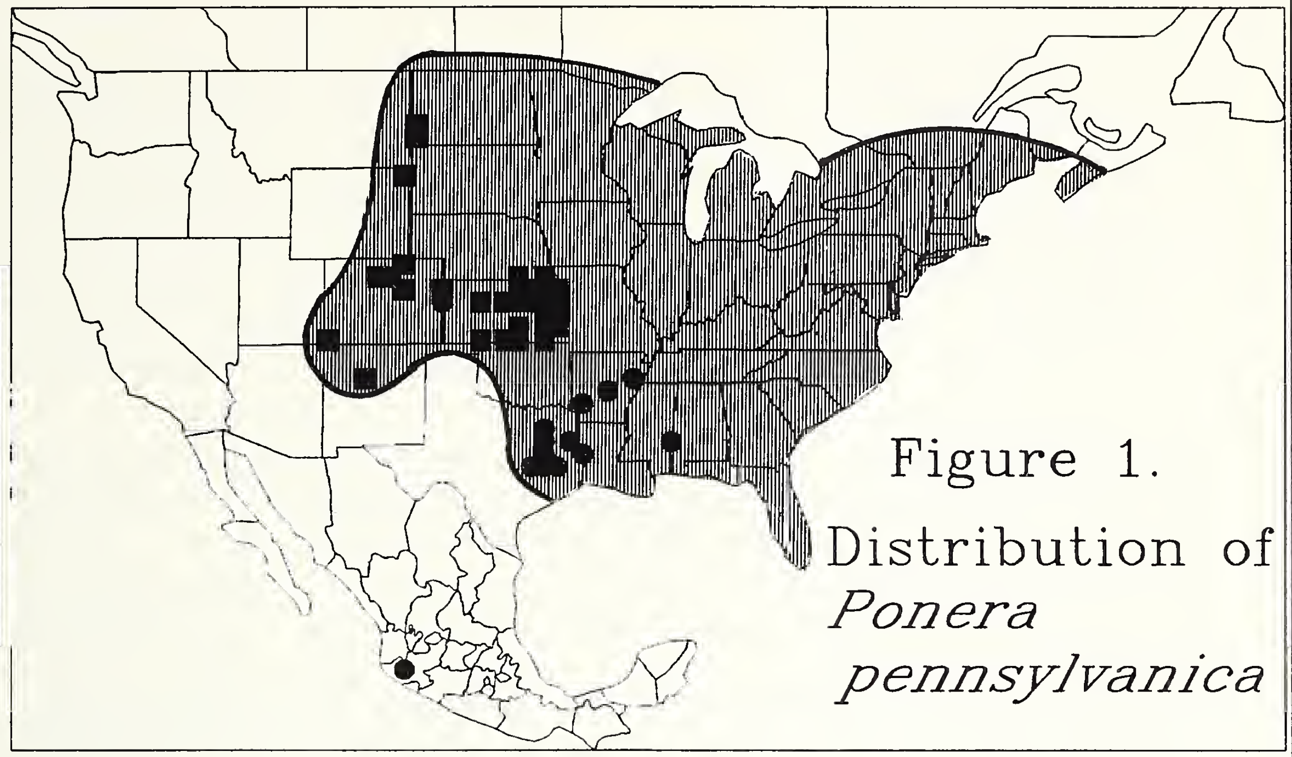

Figure 1.
Distribution of
Ponera pennsylvanica

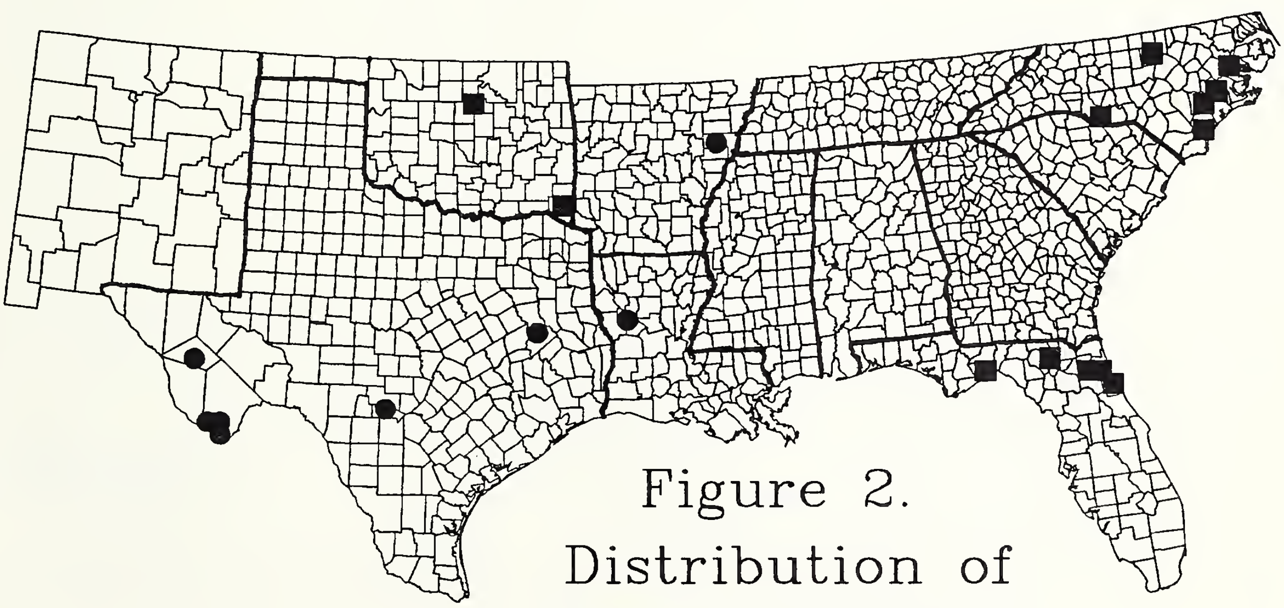

Figure 2.
Distribution of
Ponera exotica

single worker was collected in Mexico: MICHOACAN: 10.5 km N Cheran, 28-vii-1988, 2,255 meters, R. Anderson.

Ponera exotica also appears to be widely distributed in the United States, at least from western Texas north to Oklahoma, east to North Carolina and south to Florida. It probably occurs in the mountains of northern Mexico. It is common in leaf litter in the montane forests of Big Bend National Park, Texas. New localities include: ARKANSAS: Cross Co., Village Creek State Park. LOUISIANA: Natchitoches Parrish, Kisatchie National Forest, Red Bluff Camp. TEXAS: Bandera Co., Lost Maples State Natural Area. Brewster Co., Big Bend National Park (Cattail Falls, Pine Canyon, Oak Canyon). Houston Co., Big Slough Wilderness. Jeff Davis Co., 3.4 km NE Fort Davis.

Both species were found in the same samples at two localities (AR, Cross Co. and TX, Houston Co.). *Ponera pennsylvanica* appears to be a widely distributed eastern species, while *P. exotica* is a more restricted southeastern species (Figs. 1 and 2).

We know almost nothing about the roles these ants play in ecosystems, but they are apparently predators (Bechinski and Pedigo, 1981), especially on termites (Escoubas et al., 1987). Nests of *P. pennsylvanica* occur in shaded areas in or near deciduous forests under stones and in decayed logs (DuBois, 1985). Males and females have been collected in nests from July to September (DuBois, 1985). Both species are common and large numbers can be found by intensive collecting, especially with litter and soil extractions. More intensive collecting could easily reveal more details of their habits and distributions.—*William P. MacKay and Robert S. Anderson, Laboratory for Environmental Biology, Department of Biological Sciences, The University of Texas, El Paso, Texas 79968 (WPM), and Canadian Museum of Nature, Ottawa K1P 6P4, Canada (RSA).* Please correspond with William P. MacKay at the University of Texas.

Our research was supported by the Regents Appropriations–Faculty Research grant #083-50-794-23 of the University of Texas. Voucher specimens are deposited in the Texas A&M University insect collection and in the Harvard Museum of Comparative Zoology.

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Received 30 November 1989; accepted 13 March 1991.

J. New York Entomol. Soc. 99(4):699–700, 1991

NOTES ON THE BIOLOGY AND BEHAVIOR OF *EUPASTRANAIA FENESTRATA* MÉNÉTRIÉS (LEPIDOPTERA: PYRALIDAE: MIDILINAE)

There is little knowledge about the biology of the Midilinae, a small subtropical subfamily of Pyralidae. According to Munroe (1970), 45 species in seven genera are known. Munroe adds that the adults are sluggish and weakly fototatic, making them rare in collections. The only immature record known is that of the larva of *Cacographis osteolalis* Lederer as a borer in *Colocasia* (Araceae) (Munroe, 1970).

In this note we present the first host record for *Eupastranaia fenestrata* Ménétriés larvae and some information about its biology and behaviour.

This study was carried out in the "restinga" (coastal scrub) of Barra de Maricá, Rio de Janeiro State, Brasil (22°57′S, 42°50′W) where *Philodendron corcovadense* Kunth (Araceae) is the host of *E. fenestrata.* According to Munroe (1970) this moth species occurs from southern Brazil to northern Argentina.

The moth lays single eggs on the upper or lower surface of the leaves. The newly hatched larva bores into a petiole or into the leaf bud. The third instar larva moves to the apical portion of the stem, bores into it and stays there until adult emergence. During larval development a chamber is formed and frass is placed outside through the larval penetration hole. Larval development lasts approximately 41 days (N = 15) with seven instars, and the pupal stage lasts approximately 25 days (N = 3).

A few *E. fenestrata* eggs were parasitized by *Telenomus californicus* species group (Hymenoptera: Scelionidae), a gregarious parasitoid.

When the larva starts feeding activity inside the stem the plant apical growth is stopped, resulting in a compensatory growth response. A lateral stem bud starts to grow just below the larva chamber causing an abnormal architecture in *P. corcovadense* (Fig. 1).

In order to test the nature of the plant response to larval feeding, fifteen apical shoots of *P. corcovadense* were removed. After 60 days, 87% of the plants produced lateral stems and only 7% of the plants in the control group produced lateral stems, thus showing the mechanical nature of plant response.

Voucher specimens of *E. fenestrata* are deposited in the Museu Nacional do Rio de Janeiro, Rio de Janeiro, Brasil, and ones of the *Telenomus californicus* species group are in the Museu de La Plata, Argentina.—*Marina C.P. Pimentel, Margarete*

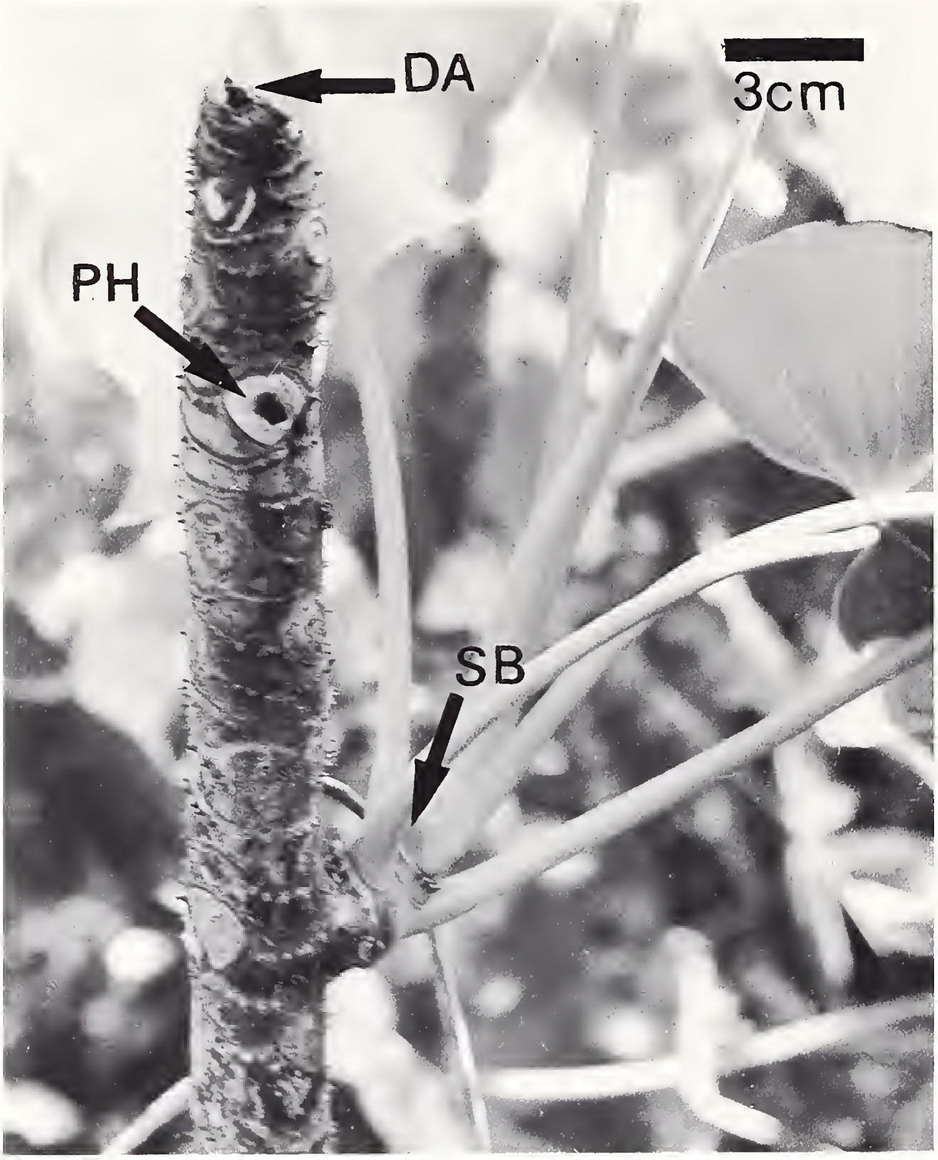

Fig. 1. *Philodendron corcovadense* structure infested by larva of *Eupastranaia fenestrata.* Note the dead apex (DA) and the stem bud (SB) grown below the larval penetration hole (PH).

V. Macêdo, and Ricardo F. Monteiro, Universidade Federal do Rio de Janeiro, I.B., Departamento de Ecologia, CP 68020, Ilha do Fundão, CEP 21941, Rio de Janeiro, RJ, Brasil.

ACKNOWLEDGMENTS

Dr. V. O. Becker (EMBRAPA/Brasília, Brasil) provided the moth identification, assisted with literature and made critical review of the manuscript. Dr. M. S. Loiácono (Universidad Nacional de La Plata, La Plata, Argentina) provided the parasitoid identification. An anonymous reviewer made valuable criticism on the manuscript. M. N. Coelho (Jardim Botânico, Rio de Janeiro, Brasil) helped in the plant identification. This study received financial support from FINEP and CNPq scholarships to M.C.P. Pimentel.

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Received 28 August 1990; accepted 20 June 1991.

J. New York Entomol. Soc. 99(4):701, 1991

DESIGNATION OF A TYPE SPECIES FOR *MACROCHLIDIA* BROWN (LEPIDOPTERA: TORTRICIDAE)

In my recent description of *Macrochlidia* Brown (1990, J. New York Entomol. Soc. 98:369–375), I inadvertently failed to designate a type species for the genus. In order to validate the genus in conformance with the International Code of Zoological Nomenclature, I hereby designate *Macrochlidia major* Brown, 1990, as the type species of the genus. I thank Kevin Tuck, British Museum (Natural History), for pointing out this significant (and embarassing) shortcoming in the description of the genus.—*John W. Brown, Entomology Department, San Diego Natural History Museum, P.O. Box 1390, San Diego, California 92112.*

CORRIGENDUM

J. New York Entomol. Soc. 99(4):701, 1991

Corrections to Schwartz, M. D. 1989. New records of Palearctic Heteroptera in New York state: Microphysidae and Miridae. J. New York Ent. Soc. 97:111–114.

In which it is stated that the holotype of the microphysid species, *Chinaola quercicola* Blatchley, was apparently destroyed in a flood at the Department of Entomology, Purdue University. Subsequently, T. J. Henry (pers. comm.) informed the author that the type specimen was located in excellent condition in the C. J. Drake Collection of the U.S. National Museum of Natural History, Washington, D.C.

BOOK REVIEWS

J. New York Entomol. Soc. 99(4):701–703, 1991

Moths of Australia.—I. F. B. Common. 1990. E. J. Brill Publishers, Leiden. 535 pp. $171.43.

Although generally acknowledged as one of the largest insect orders, estimates of total species diversity for the Lepidoptera vary. According to Nielsen (1989) there are somewhere around 250,000 species, while Common in *Moths of Australia* uses the figure 160,000. Recent compilations for the butterflies suggest approximately 18,000 species (Robbins, 1982; Shields, 1989). Based on these estimates, moths thus constitute between 89 and 93 percent of all species of Lepidoptera whereas butterflies make up only between 7 and 11 percent. Nevertheless, our current understanding of butterfly systematics and biology is much more advanced than that for any group of moths. For example, the theory of coevolution was modeled on butterflies and their host plants (Ehrlich and Raven, 1964), and a great deal of subsequent plant/insect research has focused on butterflies. However, we know relatively little concerning the host plant biology of moths.

A great deal more research on moths is required before it will be possible to understand either the biodiversity or the evolution of the Lepidoptera. This deficiency has implications beyond academia; moths far outweigh butterflies in terms of their economic importance. Field guides and general treatments of moths are few, a situation that has made it difficult to generate interest among amateurs, as well as among biologists other than taxonomists. Our general knowledge of the Lepidoptera has suffered as a result. Ian Common's book, *Moths of Australia,* goes a long way toward alleviating some of these problems.

Before *Moths of Australia* was published, it was remarkable how often I found myself using the Lepidoptera section in *The Insects of Australia* (Common, 1979) to learn about various aspects of biology, classification, and morphology. Common's new book takes that chapter several giant leaps forward. With over 22,000 species of Lepidoptera in Australia, the book does an admirable job of providing thorough coverage. Habitus photographs (taken by Ederic Slater) are numerous and they are of excellent quality. These include 32 color plates of adults and larvae and 39 pages of black and white photographs of adults and larvae. According to the jacket write-up, over 1,000 species are illustrated.

Part One, entitled "Moths and Their Environment," comprises overviews, all of which are extremely well done, on structure and life history, biology, economic significance, evolution, and geographical distribution. This section provides an important source for students, non-specialists, and specialists interested in Lepidoptera. At the end of Part One there is a family classification of moths (which will appear in the forthcoming *Checklist of the Lepidoptera of Australia*) for the world fauna. In Part Two, the entire moth fauna of Australia is treated in phylogenetic order according to this classification. Although detailed treatment is restricted to Australian groups, families occurring outside the region are also mentioned. For example, the Dioptidae (New World) and Thyretidae (Africa) are briefly discussed in the introduction to the superfamily Noctuoidea.

The chapters in Part Two consist essentially of superfamily groupings (with a brief introduction for each). Within chapters the included families are discussed in order. For each family there is a character diagnosis for adults, larvae, eggs, and pupae, as well as a fairly lengthy discussion concerning the biology of the group. Groups are given fairly detailed treatment, and for the families I know, coverage is complete and it demonstrates amazing taxonomic insight. The book includes more than 500 high quality line drawings of male and female genitalia, wing venation, and pupae. Use of pupae is especially noteworthy considering the lack of attention given to this life stage in most other books.

The reference section includes close to 600 citations. Although most of these relate to Australian moths, many others are general references. Based on this section alone the book is a fantastic source. In addition, there is a glossary with more than 200 terms concerning morphology and biology of the Lepidoptera. Appendix A provides a useful introduction to techniques of collecting, preparing, rearing, and photographing. *Moths of Australia* serves as a model for general texts on other insect groups, or on any group of organisms for that matter. The book left me with the impression that it was written by an expert in the true sense of the word.

There are only two ways that I can imagine improving the volume. The first is relatively trivial. Appendix B, called a "Food Plant and Larval Host List," contains

twelve pages of host records. It is arranged in the following manner. Plant families are laid out in alphabetical order, and under each family there is a list of plant genera (also arranged in alphabetical order). For each plant genus the moth species recorded as feeding on that genus are listed, again in alphabetical order, but with no family affinity specified. This is roughly the same format W. T. M. Forbes used in his series of publications on *Lepidoptera of New York and Neighboring States.* Having used the host lists in both books, I find them somewhat frustrating. Most biologists are interested in host lists for particular moth or butterfly taxa. This type of information is difficult to retrieve from Common's Appendix B. First, one would need to use the forthcoming checklist of Australian moths to make a list of generic names for the moth group of interest, then one would have to search manually through Appendix B to compile a table of host plants according to moth taxon. In future editions of *Moths of Australia,* it would be helpful to have an "Appendix C" with host plants listed for each moth family.

The second way the book could be improved is slightly more radical, but it is absolutely necessary. The price should be lowered! My copy from E. J. Brill Publishers has a list price of $171.43. Having extolled the virtues of this book in terms of its quality and its extreme usefulness to students and researchers, such a high price makes the volume inaccessible for many people, a distressing state of affairs. Book prices have been known to drop, and I hope this one follows that pattern. A realistic price would be $65 or $70.—*James S. Miller, Department of Entomology, American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024.*

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J. New York Entomol. Soc. 99(4):703–704, 1991

The Genetics of Social Evolution.—M. D. Breed and R. E. Page, Jr. (Eds.). 1989. Westview Press, Boulder, Colorado, USA. 213 pp. $35.95.

The unifying theme in this collection of ten papers is how patterns of genetic variation relate to insect sociality, both contemporary processes of social homeostasis and the evolutionary history of group living and reproductive division of labor. All papers pertain primarily or entirely to Hymenoptera. Some of the papers are data-rich, some mainly theoretical. The emphasis is strongly population genetic, and when evolutionary history is discussed, only one paper is truly comparative, the rest relying on more traditional "plausible scenarios" to support various theories of social evolution.

Breed's introduction provides a concise review of the issues and terminology, clearly from a population geneticist's point of view. Papers by Page *et al.,* Owen, and Robinson and Page summarize recent work on the genetics of honeybees, in particular exploring the implications of genetically distinct subfamilies of workers within colonies. The role of colony-level vs. individual selection in maintaining social traits is explored. I was intrigued by a model explaining division of labor, in which genetic variation in response thresholds to stimuli determine which bees carry out certain tasks. As a behavioral model it explains very well why my wife takes out the garbage and I wash the dishes. Ross describes strong heterogeneity in the reproductive output of polygynous fire ant colonies (results which are largely repeated in other publications, but are nicely summarized here). Kukuk presents relatedness data for aggregations, neighborhoods, and colonies of the primitively eusocial bee, *Dialictus zephyrus,* suggesting that genetic viscosity is sufficient for kin selection to be effective.

Research on the evolution of sociality has focused on degrees of relatedness and kin selection, a result of the correspondence between haplodiploidy (and consequent high relatedness of sisters) and the multiple occurrence of sociality in the Hymenoptera. However, increasing discovery of multiple mating by queens, polygyny, and genetically disparate workers is eroding the credibility of this theory. Rather than dwelling on the individual reproductive cost of group living, the papers by Strassmann and Queller, stemming from their extensive work with the ecology of vespid wasps, emphasize the other side of the equation: the demographic benefit. A strong demographic benefit offsets the need for high relatedness in the evolution of sociality.

However, if ecological factors do favor group living, the question remains: Why so frequently in the Hymenoptera? Rather than haplodiploidy, could it be some other Hymenopteran feature that facilitates the evolution of sociality. For example, could some peculiarity of Hymenopteran individual recognition encourage group formation? Nestmate recognition is an understudied phenomenon, yet is a fundamental feature of social systems. Mintzer, in a novel and important study, demonstrates genetic components of nestmate recognition in Acacia ants, presents several alternative genetic models, and compares observed and predicted patterns.

Finally, Ward's paper on speciation, polygyny, and social parasitism in ants deserves special mention. A much touted but rarely applied approach to the study of evolutionary history is to map behavioral traits of interest onto phylogenies derived from independent (usually structural and/or genetic) data. Ward has used this approach to answer the questions 1) is polygyny a species-level trait (no, degree of polygyny is intraspecifically variable), and 2) are social parasites sister species of their hosts, and thus definite examples of sympatric speciation (no). The general treatment of speciation in ants is particularly valuable to myrmecologists. This paper seems out of place in this volume, and I fear will get less attention as a result.

The printing is clear and uniform throughout, I detected few typographical errors, and there is a thorough index.—*John T. Longino, Allyn Museum of Entomology, 3621 Bay Shore Rd., Sarasota, Florida 34234.*

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We take this opportunity to thank Dr. David A. Grimaldi for serving as our Book Review Editor during the past four years. Dave actively sought books for review that he felt would be of interest to our membership, and he succeeded in getting reviewers to submit their reviews in a timely manner. For that reason we have consistently beaten the "big" journals to press with insightful critical appraisals of entomological books.

At the same time, we welcome Dr. James S. Miller as our new Book Review Editor starting in 1992. We appreciate Jim's willingness to serve the Society in this capacity. If you would like to review a book, you may convey your interest to him.

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Journal of the New York Entomological Society

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